

Abstract.—The endemic North Pacific pleuronectid genus *Lepidopsetta* Gill is revised to include three species: *L. bilineata* (Ayres), *L. polyxystra* n. sp., and *L. mochigarei* Snyder. Adults of *L. bilineata* can be distinguished by a low gill-raker count and high supraorbital pore count; larvae may be distinguished by four dorsal midline melanophores, heavy finfold pigment, a short snout-to-anus length, and a deep body. The species ranges from Baja California to the eastern Aleutian Islands and the extreme southeastern Bering Sea. Adults of *L. mochigarei* are distinguished from all other members of *Lepidopsetta* by higher scale and preopercular pore counts and lower gill-raker and supraorbital pore counts. Larvae are similar to larvae of *L. bilineata* but can be distinguished by their postanal pigment pattern and melanophores on pectoral-fin rays. *Lepidopsetta mochigarei* ranges from the southern Sea of Okhotsk to Korea. Adults of *L. polyxystra* n. sp. are diagnosed by a high gill-raker count and low supraorbital pore count; larvae are diagnosed by two dorsal midline melanophores, light finfold pigment, long snout-to-anus length, and a slender body. The species is found from Puget Sound through the Bering Sea and Aleutian Islands to the Kuril Islands, overlapping with *L. bilineata* from the extreme southeastern Bering Sea to Puget Sound and with *L. mochigarei* in the southern Sea of Okhotsk. Synonymies, diagnoses, descriptions, and geographic distributions are provided for adults and larvae of all species; keys are provided for adults. Descriptions of early juveniles of eastern North Pacific species are also presented. Under the name of *L. bilineata*, *L. polyxystra* n. sp. has been the subject of many studies of eastern North Pacific *Lepidopsetta*. All previous studies of specimens from the southeastern Bering Sea into Puget Sound should be considered applicable at the generic level only, unless voucher specimens are verifiable.

Revision of the genus *Lepidopsetta* Gill, 1862 (Teleostei: Pleuronectidae) based on larval and adult morphology, with a description of a new species from the North Pacific Ocean and Bering Sea

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The flatfishes (Pleuronectiformes) of the eastern North Pacific Ocean constitute a major component of the commercial fisheries of the region. In the Bering Sea, which encompasses the largest fisheries resource of the United States, the rock soles of the genus *Lepidopsetta* are the second most abundant flatfishes and the third most abundant commercial groundfish species, second only to yellowfin sole (*Limanda aspera*) and walleye pollock (*Theragra chalcogramma*) (NMFS, 1999).

At the species level, eastern North Pacific pleuronectids have been considered well known. Nearly all species were recognized and described during the latter half of the 1800s, primarily through the activities of California ichthyologists. Among the names that remain valid, the last species to be described was *Limanda sakhalinensis* Hubbs, 1915, although in the western Pacific *Microstomus shuntovi* Borets, 1983, was most recently described from the northwestern Hawaiian ridge. However, these earlier works were based on adult morphology, and only recently has a knowledge of the ontogeny of these species been acquired. Among the descriptions of early life history stages of eastern North Pacific pleuronectids, one morphological form could not be traced to a recognized species. Examination of this form led to the following revision of the genus *Lepidopsetta*.

Four nominal species have been described and allocated to the genus *Lep-*

idopsetta: *Platessa bilineata* Ayres, 1855a, was described from San Francisco material, and apparently without the knowledge of Ayres' slightly earlier description, a specimen collected near Puget Sound was described as *Platichthys umbrosus* Girard, 1856. Gill (1862) erected *Lepidopsetta* to contain *Platichthys umbrosus* and later (1864) indicated that *Platessa bilineata* Ayres, 1855a, was allied and perhaps congeneric. Lockington (1879b) published a redescription of *L. umbrosa*, describing the misidentified new species *Isopsetta isolepis* (Lockington, 1880a), which he ultimately removed from *Lepidopsetta* to his new genus *Isopsetta* (Lockington, 1883). In his description of *Lepidopsetta isolepis*, he treated *Platichthys umbrosus* Girard as a synonym of *L. bilineata*. Nearly 20 years after Gill's erection of *Lepidopsetta*, Cope (1873) described *Pleuronectes perarcuatus* from Alaska, later considered a synonym of *L. bilineata* by Jordan and Gilbert (1881). Jordan and Evermann (1898) considered each of these nominal species members of *Lepidopsetta* and further as synonyms of *L. bilineata*, although they recognized the northern populations ("Puget Sound and northward") as *L. bilineata umbrosa*. Finally, Japanese *Lepidopsetta* were described by Snyder (1911) as *L. mochigarei* and Jordan and Hubbs (1925) considered all Japanese *Lepidopsetta* to be representatives of this species.

More recently, the genus has been envisioned as containing either two spe-

cies, *L. bilineata* of the eastern North Pacific Ocean and Bering Sea and *L. mochigarei* of the western North Pacific around Japan (Hubbs, 1915; Sakamoto, 1984b), or a single species, *L. bilineata*, with two subspecies *L. b. bilineata* and *L. b. mochigarei* in the Bering Sea and western Pacific (Taranets, 1937; Schmidt, 1950). A third subspecies in the southeastern North Pacific was recognized by Moiseev (1953) and Wilimovsky et al. (1967). Although both authors split eastern Pacific populations into two subspecies, Moiseev (1953) considered the northern subspecies to be *L. b. bilineata* and the southern subspecies to be *L. b. umbrosa*, whereas Wilimovsky et al. (1967) applied the names *L. b. perarcuata* and *L. b. bilineata* to northern and southern populations, respectively.

Our study arose from an examination of collections from ichthyoplankton surveys conducted from the Bering Sea to northern California by the Recruitment Processes Task (referred to simply as "Task" in the following account) of the Alaska Fisheries Science Center (AFSC). In 1985, ichthyoplankton taxonomists began to routinely separate an unidentified pleuronectid from numerous collections. Larvae from the developmental series of this unidentified pleuronectid most closely resembled larvae previously described as *Psettichthys melanostictus* (Hickman, 1959; Pertseva-Ostroumova, 1961) and, for the following few years, larval pigment patterns and morphological characters were used to separate what were then considered *Psettichthys* into two readily distinguishable morphotypes. Thus in 1986, an early draft of the Task's laboratory guide (Matarese et al., 1989) included illustrations of an unidentified series referred to as a variant of *Psettichthys* ("*Psettichthys* 2").

During winter and spring 1987, larvae of both morphotypes of "*Psettichthys*" were collected from Puget Sound and reared through transformation and settlement stages, and upon examination of the reared juveniles, Kendall and Matarese¹ determined that larvae previously referred to as "*Psettichthys* 2" were, in fact, another form of *Lepidopsetta*. From the early results of this work, Matarese et al. (1989) decided to include a partial description of the unknown pleuronectid (referred to as "*Lepidopsetta* 2") and compared various stages with larvae of *Psettichthys* and other *Lepidopsetta*. Mulligan et al. (1995) finally verified the identity of *Lepidopsetta* 2 by rearing larvae spawned from *Lepidopsetta* adults collected in Puget Sound and conducted a morphological study of adults. Although they reported significant heterogeneity in shape, structure, and allozymes, they recommended the retention of Wilimovsky et al.'s (1967) subspecies designations.

Although previous authors (Townsend, 1936, 1937; Wilimovsky et al., 1967; Mulligan et al., 1995) concluded that observed variation represented a cline smoothly grading from California through the Bering Sea to Japan and supported subspecific designations, new data became available in 1992 with the development of a fishery for *Lepidopsetta* in the northern Gulf of Alaska. Domestic fisheries observ-

ers (see "Acknowledgments" section) experienced in sampling in the Bering Sea flatfish fisheries began to report the presence of two syntopic adult forms of *Lepidopsetta* in the northern Gulf of Alaska, one distinctly different from the form in the eastern Bering Sea. These observations spurred a further examination into the morphological differences of all life stages of *Lepidopsetta*. Our revision therefore incorporates evidence from adult, juvenile, and larval morphology and distribution to support the recognition of three species, one described as new, in the North Pacific. We describe morphological variation in adults, juveniles, and larvae; differentially diagnose adults, juveniles, and larvae; and describe geographic and bathymetric distributions of the three species.

Materials and methods

Unless indicated otherwise, standard length (SL) is used throughout. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988), as modified by Poss and Collette (1995), except for the Kamchatka Institute of Ecology, abbreviated as KIE.²

Adult morphology

Meristic data, except gill-raker counts, and morphometric data were taken from the ocular-side of adult material, following Hubbs and Lagler (1958) with the following exceptions. Standard, head, and snout length were measured from the anterior margin of the maxilla, with the mouth closed. Body depth was the greatest depth measured at the origin of the anal fin. Head length included only the opercle and not the opercular membrane. Snout length was measured to the anterior edge of the dorsal orbit. Cheek length was the greatest distance from the posterior rim of the ventral orbit to the edge of the preopercle, often the posterior angle of the preopercle. Interorbital width equals the least bony width. Pectoral-fin length was the length of the longest ray, often the third ray, and was measured for both ocular-side and blind-side fins. Lateral-line arch length was the distance between anterior and posterior flexion points, and this straight line was used as the base for the depth measurement. Greatest caudal peduncle depth was measured at the base of the caudal fin.

All rayed elements were included in counts of fin rays. The last two rays of the dorsal and anal fins were counted separately. Scales above the lateral line were counted on a diagonal at the greatest depth between the dorsal-fin base and lateral line. Scales below the lateral line were counted from the anal-fin origin on a diagonal to the lateral line. Total scales above and below the lateral line is the sum of the two counts. Cheek scales were counted at greatest cheek length. Ocular-side suborbital pores were counted

¹ Kendall, A. W., Jr., and A. C. Matarese. 1987. Unpubl. data. Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

² Sheiko, B. 1997. Personal commun. Kamchatka Institute of Ecology, Partizanskaya 6, Petropavlovsk-Kamchatsky 683000, Russia. Present address: Department of Ichthyology, Zoological Institute, Russian Academy of Sciences, Universitetskaynab. 1, St. Petersburg 199034, Russia.

from the first pore branching from the temporal canal to the anteriormost pore; all pores were counted, including those dorsal and ventral to the canal. Blind-side suborbital pores were counted from the first pore branching from the postorbital canal to the anteriormost pores. Pore counts of the dorsal anterior and posterior branches of the accessory dorsal branch of the lateral line (ADB) began with the first pore of each branch and did not include the single pore typically found at the intersection of the two branches. Supraorbital pores include the first pore dorsal to the postorbital canal and include those pores at the posterior rim of the dorsal orbit (Fig. 1). Preopercular pores begin with the first pore posterior to the mandibular articulation and end at the last pore before the temporal canal. Caudal-fin terminology follows Sakamoto (1984a).

Larval collections

Most data were garnered from samples collected by the AFSC with standard bongo gear during ichthyoplankton surveys of the Bering Sea and Gulf of Alaska (1971–1994, Table 1, Appendix Table 1). In most cases, the identities of specimens collected prior to 1985 (when the unidentified pleuronectid developmental series was first separated) have been verified. All larval specimens used for illustrations and morphological descriptions have been cataloged at the University of Washington Fish Collection (UWFC); other material will be archived at the UWFC as well (see Appendix Table 1). Additional data for *Lepidopsetta* in Canadian waters were obtained from the Canadian Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo (W. Shaw), and Vancouver Public Aquarium (J. Marliave; these specimens are now deposited at UWFC). The Washington Department of Fisheries also provided distribution and life history data for Puget Sound.³ In addition, dip-net sampling in Puget Sound conducted by the AFSC from 1985 through 1995 resulted in 16 collections of *Lepidopsetta* larvae (Busby et al., 2000). Two larvae from the Washington, Oregon, and northern California survey area were examined—the only two *Lepidopsetta* larvae collected during the eight years (from 1980 to 1987) during which the AFSC conducted ichthyoplankton cruises in the region. Geoff Moser, NMFS Southwest Fisheries Science Center (SWFSC), provided data for *Lepidopsetta* collected during California Cooperative Fisheries Investigations (CalCOFI) cruises conducted along the coast of California.

Identification of juveniles

Recently transformed juveniles present particular problems in identification because adult characters, such as meristics and pigment patterns, are not completely developed and some aspects of larval shape, structure, and pigment patterns are retained. Thus, early juveniles (approximately 20–35 mm SL) were identified by a combi-

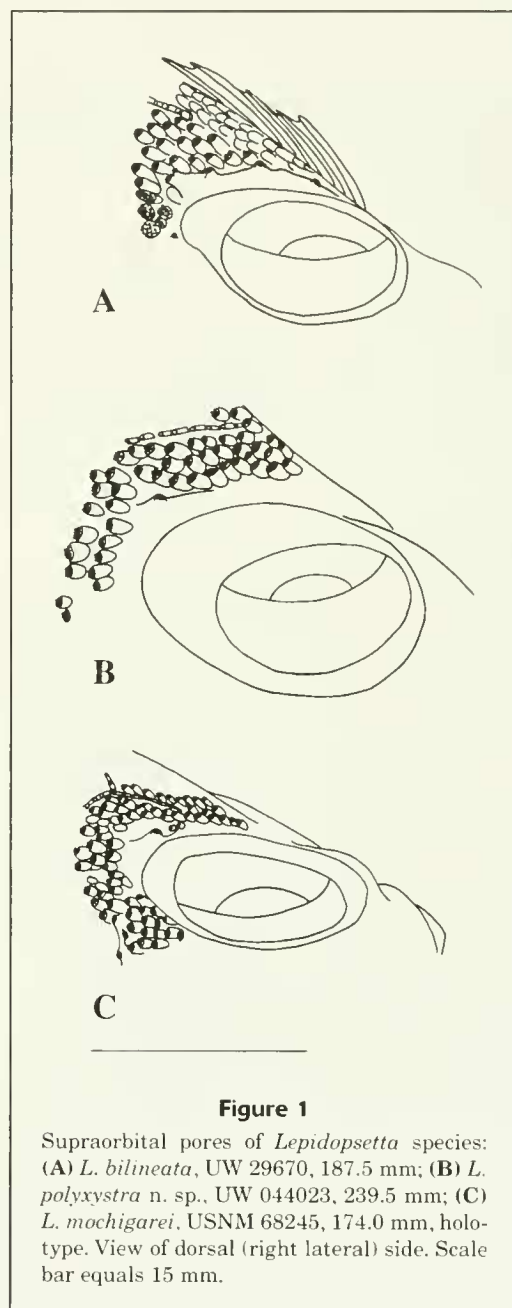


Figure 1

Supraorbital pores of *Lepidopsetta* species: (A) *L. bilineata*, UW 29670, 187.5 mm; (B) *L. polyxystra* n. sp., UW 044023, 239.5 mm; (C) *L. mochigarei*, USNM 68245, 174.0 mm, holotype. View of dorsal (right lateral) side. Scale bar equals 15 mm.

nation of characters, including gill-raker counts of the first arch, larval pigment characters retained on the blind side, and size at transformation. Although gill rakers were not fully formed, specimens with counts greater than seven on the lower arch were assumed to be the new species. Juveniles with counts of seven or less were identified in conjunction with other characters. Postsettlement juveniles greater than 30 mm SL were separated by using the above characters in addition to counts of the number of supraorbital pores. *Lepidopsetta bilineata* typically has 4–6 head pores along the supraorbital canal, whereas the new species typically has 1–3. Differences in gill-raker structure useful in distinguishing adults are usually not evident at sizes less than 200 mm SL.

³ Penttila, D. 1996. Personal commun. Puget Sound Forage Fish Unit, Washington Department of Fish and Wildlife, 1702 Anderson Road, Bay 4, Mt. Vernon, WA 98173.

Table 1

Collections of *Lepidopsetta* larvae examined for this study. AFSC = Alaska Fisheries Science Center, Seattle, WA; VPA = Vancouver Public Aquarium, Vancouver, BC; PBS = Pacific Biological Station, Nanaimo, BC; CalCOFI = California Current Oceanic Fisheries Investigations, La Jolla, CA.

General location	Source of data	Years	Months sampled	No. of samples
Bering Sea	AFSC	1971, 1977, 1979, 1988, 1992–94	Apr–Aug	152
Gulf of Alaska	AFSC	1972, 1978–79, 1981–94	Mar–Oct	1896
British Columbia	VPA, PBS	1983–88, 1991–93	Mar–July	72
Puget Sound	AFSC	1985–95	Mar–July	16
WA, OR, and N. CA	AFSC	1980–87	Apr–May	2
California	CalCOFI	1951–84	Feb–July	21

Identification of larvae

Identification of *Lepidopsetta* larvae was accomplished by a variety of methods because the more traditional serial approach was not possible. Initially, our unidentified pleuronectid series was grouped together on the basis of a continuous sequence of shared characters. This series, however, could not be linked with a recognized pleuronectid taxon whose larvae had not already been described. The unidentified series (*Psettichthys* 2) was similar to larvae previously described for *P. melanostictus*. Larvae of *Psettichthys* 2 were determined to be *Lepidopsetta* by rearing wild-caught larvae¹ and finally confirmed to be *Lepidopsetta* by rearing larvae spawned from *Lepidopsetta* adults collected in Puget Sound (Mulligan et al., 1995).

Nomenclature of larval developmental stages follows Kendall et al. (1984) where each stage is based on widespread, fundamental features of development. The early life history stages used in our study were based on the flexion of the notochord that accompanies the hypochordal development of the homocercal caudal fin. The onset of the juvenile stage is defined in our study as completion of eye migration and attainment of the adult complement of fin elements. Early juveniles (approximately 20–35 mm SL) are defined as those collected in the water column; many had remnants of larval pigmentation on their blind side. Postsettlement juveniles were collected with bottom gear and rarely retained any larval pigmentation on their blind side.

Only melanistic pigment is described in our study because formalin fails to preserve other pigments (live larvae have yellow, orange, and brown chromatophores associated with the melanophores). Previous descriptions of larval pigment patterns, particularly those of pleuronectids, have used confusing terminology. Postanal pigment patterns have been variously described as vertically oriented bands (Pertseva-Ostroumova, 1961; Moser et al., 1984; Matarese et al., 1989) and bars (Charter and Moser, 1996). The number of postanal bands and bars may or may not include the caudal or terminal notochord pigment. For clarity, in the descriptions of pigment patterns, the terms “band” and “bar” refer to aggregations of melanophores that approximate vertically oriented rectangles (including

the caudal pigment). A band is always complete and a bar incomplete. A “stripe” approximates a line or elongate rectangle and is horizontally oriented. A “spot” is an approximately circular aggregation of melanophores. A “patch” is any other distinguishable aggregation of melanophores.

Larval morphology

A total of 115 eastern North Pacific *Lepidopsetta* larvae were measured with a calibrated digital image analysis system (larvae of the western North Pacific *L. mochigarei* were not available). This system consists of a video camera attached to a dissecting stereomicroscope or camera lens, a microcomputer with digital imaging board, and a video monitor. All measurements of larvae were taken from the left side. Unless otherwise noted, standard length (SL) is used throughout and is defined in our study as the length from snout tip to notochord tip (prior to development of the caudal fin) or to the posterior margin of hypural elements. Other measurements are defined as follows: head length (HL), snout tip to posterior edge of opercle (to pectoral-fin base in small larvae before opercular margin is visible); snout length (SNL), snout tip to anterior margin of orbit; orbit length (OL), greatest length of orbit; body depth (BD), vertical distance from dorsal to ventral body margin at a vertical line through center of anal opening; snout-to-anus length (SAL), distance along body midline from snout tip to a vertical line through center of anal opening. Standard proportional measurements were calculated (Table 2).

Distributional analysis of larvae

The dataset used for mapping and calculation of mean density of larvae (number per 10 m²; Appendix Table 1) was a subset of the AFSC ichthyoplankton historical database (1972–1994) from the Bering Sea and Gulf of Alaska. This subset included all reidentified samples that had been originally identified as *Psettichthys* 2, *Lepidopsetta* 2, and *L. bilineata* and thus provided the only historic distributional records for larvae of *L. polyxystra* n. sp. Maps of material examined and distribution and mean density

Table 2

Proportional measurements for *Lepidopsetta* larvae. SL = standard length; HL = head length. Statistical significance of raw data was evaluated by an ANCOVA analysis. See Table 10 for *P*-values. NS = not significant; S = significant.

Developmental stage	<i>L. polyxstra</i> n. sp.	<i>L. bilineata</i>	Significance
Yolksac			
Sample size	6	13	
Snout-to-anus length /SL	32.1 ±1.7 (30.6–34.8)	32.9 ±1.8 (30.1–36.8)	NS
Body depth/SL	3.8 ±0.6 (2.7–4.3)	4.7 ±0.8 (3.9–6.7)	S
Head length/SL	11.6 ±1.0 (10.1–12.6)	13.3 ±1.4 (10.0–15.1)	NS
Snout length/HL	24.7 ±2.4 (21.2–27.1)	22.6 ±7.8 (13.1–36.5)	NS
Orbit length/HL	51.8 ±5.6 (43.8–58.9)	51.9 ±6.6 (36.7–61.5)	NS
Preflexion			
Sample size	11	13	
Snout-to-anus length /SL	33.5 ±1.3 (32.3–36.0)	30.7 ±2.3 (26.8–34.3)	S
Body depth/SL	4.8 ±0.7 (3.2–5.8)	5.0 ±0.9 (3.3–6.7)	NS
Head length/SL	13.0 ±1.3 (10.6–15.6)	12.7 ±1.8 (10.4–15.8)	NS
Snout length/HL	20.5 ±5.3 (13.3–29.7)	23.5 ±6.3 (15.1–35.8)	NS
Orbit length/HL	48.1 ±6.7 (34.1–61.9)	45.3 ±5.6 (37.1–53.0)	S
Flexion			
Sample size	26	17	
Snout-to-anus length /SL	35.5 ±2.5 (31.3–40.0)	33.8 ±2.1 (29.9–38.2)	S
Body depth/SL	10.5 ±4.1 (4.6–18.0)	11.1 ±5.1 (5.5–21.9)	S
Head length/SL	19.1 ±3.6 (13.3–26.4)	17.9 ±3.0 (14.6–24.4)	NS
Snout length/HL	20.5 ±3.3 (12.8–26.2)	22.5 ±4.7 (13.5–29.3)	NS
Orbit length/HL	31.1 ±6.9 (20.6–44.9)	33.6 ±4.1 (27.8–40.6)	NS
Postflexion			
Sample size	10	19	
Snout-to-anus length /SL	39.3 ±3.3 (35.3–45.7)	34.6 ±2.9 (29.3–38.2)	S
Body depth/SL	28.5 ±6.4 (20.0–38.6)	35.7 ±3.0 (27.8–39.9)	S
Head length/SL	26.7 ±2.4 (22.4–30.6)	29.3 ±1.7 (26.7–32.7)	S
Snout length/HL	22.8 ±2.1 (19.3–26.0)	20.7 ±2.3 (16.8–24.2)	NS
Eye length/HL	20.9 ±2.4 (17.5–24.0)	23.8 ±3.2 (19.6–31.8)	S
Total larvae measured	53	62	

of species were generated by using the geographic information system Arc/Info and ArcView (Environmental Systems Research Institute, 1996). Tables were produced with ArcView and Systat software (SPSS, Inc., 1996). Densities were mapped by dividing the geographic area into contiguous square polygons, 625 km² each. Catches per unit of effort (CPUEs) from all tows (including 0 catches) within each square polygon were averaged, yielding a mean density. Polygons were shaded according to their mean density, or left unshaded when no tows occurred within a polygon.

Adult statistical analyses

The software programs S-Plus (Statistical Sciences, 1993) or Statgraphics Plus 2.1 (Manugistics, 1997) were used in statistical analyses performed on juveniles and adults. Unless otherwise indicated, tests were considered signifi-

cant at $P < 0.05$, as adjusted by the Bonferroni correction (Sokal and Rohlf, 1995). For all characters, Bartlett's test of homogeneity of variances (Sokal and Rohlf, 1995) was used to determine the appropriateness of an ANOVA to test for differences between species. When Bartlett's test found significant differences in variances, pairwise comparisons were made. Pairs with significant differences in variances were then tested for differences in medians by using the nonparametric Kruskal-Wallis test (Sokal and Rohlf, 1995). The following meristic characters did not differ significantly in variance among species pairs and were subjected to an ANOVA: gill rakers of the upper and lower first arch and lower second arch; dorsal- and anal-fin rays; ocular-side and blind-side pectoral-fin rays; posterior and anterior ADB pores; interorbital scales; cheek scales; scales above, below, and total around the lateral line; ocular-side and blind-side suborbital pores; supraorbital pores.

Table 3
Counts of gill rakers for species of *Lepidopsetta*.

Species	Upper first arch											
	1	2	3	4	5	6	<i>n</i>	<i>x</i>	SD			
<i>L. bilineata</i>	12	167	104	4			287	2.3	0.58			
<i>L. mochigarei</i>	1	18	8				27	2.3	0.53			
<i>L. polyxystra</i> n. sp.			135	183	15	3	336	3.7	0.61			
	Lower first arch											
	4	5	6	7	8	9	<i>n</i>	<i>x</i>	SD			
<i>L. bilineata</i>	5	105	160	17			287	5.7	0.62			
<i>L. mochigarei</i>	1	5	18	3			27	5.9	0.66			
<i>L. polyxystra</i> n. sp.			13	204	114	5	336	7.3	0.57			
	Lower second arch											
	5	6	7	8	9	10	11	12	13	<i>n</i>	<i>x</i>	SD
<i>L. bilineata</i>	1	52	170	38	12	2				275	7.1	0.76
<i>L. mochigarei</i>		2	14	10	1					27	7.4	0.69
<i>L. polyxystra</i> n. sp.			4	17	125	139	40	10	1	336	9.7	0.92

For morphometric characters, significant differences between species were identified using an ANOVA of arc-sine-transformed ratios of the measurement divided by SL or HL (Sokal and Rohlf, 1995) and an analysis of covariance (ANCOVA) with SL or HL as covariates when assumptions of homogeneity of slopes were satisfied. The following morphometric characters did not significantly differ in variances among species pairs and were subjected to an ANOVA: head length, snout length, ocular-side maxilla length, blind-side maxilla length, ocular-side mandible length, cheek length, interorbital width, dorsal orbit length, ocular-side pectoral-fin length, body depth, caudal peduncle depth, and caudal-fin length. Snout length, blind-side maxilla length, ocular-side mandible length, and interorbital width were also subjected to ANCOVA.

To aid in the discrimination and classification of species, standard principal components analysis (PCA) was conducted on all morphometric and meristic characters for adults of all species together and on the eastern North Pacific material separately. Raw morphometric data were log-transformed and the covariance matrix was subjected to PCA, as was the correlation matrix of raw meristics. Differences between species were illustrated by separately plotting principal components (PC) 2 and 3 of the morphometric analyses, PC1 and PC2 of the meristic analyses, and PC1 of the meristic analyses against PC2 of the morphometric analyses (Stauffer and Hert, 1992). For eastern North Pacific species, data points were also identified by reference to 11 geographic regions: Sea of Okhotsk, western Bering Sea, eastern Bering Sea, Aleutian Islands, Gulf of Alaska, British Columbia, Puget Sound, Washington coast, Oregon coast, California coast, and Baja California coast.

Larval statistical analyses

In an effort to identify additional characters to distinguish larvae of the two eastern North Pacific species, morphometric characters of yolk sac preflexion, flexion, and post-flexion larvae were further analyzed. Scatter plots for each measurement versus SL were made. Morphometric data were analyzed by the ANCOVA model for each parameter at each developmental stage and at all stages combined, which included species as a factor, standard length as a covariate, and a species/SL interaction (e.g. $BD = C + Species + SL + (Species \times SL)$). A residual analysis was done for each model to determine the appropriateness of the model. Whenever the interaction was not significant (at the 5% level), a reduced model was used, and the interaction was dropped and the slopes were forced to be the same ($BD = C + Species + SL$). This procedure removed the effect of SL and allowed testing for significant differences between species. When the species were significantly different, the *P*-value was reported and graphs were generated to illustrate differences between elevations of the two regressions. Principal components analysis was also used to highlight differences.

Results

Adults

All three species differed significantly from each other in three meristic characters (Tables 3–7): posterior ADB pores (Table 5), total scales above and below the lateral

Table 4
Fin-ray counts for species of *Lepidopsetta*.

Species	Dorsal-fin rays																				n	x	SD		
	64	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85				86	89
<i>L. bilineata</i>		1			4	1	6	5	10	7	15	22	21	11	8	5	3	1	1	1	4	1	127	77.14	3.57
<i>L. mochigarei</i>								1	5	3	10		3	1		3	1						27	76.52	2.46
<i>L. polyxystra</i> n. sp.	1	3	5	6	12	9	13	12	13	8	20	14	10	14	7	4	1	2					154	74.60	3.84
Species	Anal-fin rays																				n	x	SD		
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66							
<i>L. bilineata</i>								7	2	13	26	17	29	15	9	4	1	2	1	126	59.3	2.15			
<i>L. mochigarei</i>									1	3	5	4	5	6	1	1		1		27	59.6	2.02			
<i>L. polyxystra</i> n. sp.	1	3	6	4	5	6	14	20	11	17	17	20	15	9	3	2				153	57.5	3.28			
Species	Blind pectoral-fin rays										n	x	SD												
	8	9	10	11	12	13																			
<i>L. bilineata</i>				10	52	62	2	126	11.4	0.66															
<i>L. mochigarei</i>				2	17	6	2	27	11.3	0.72															
<i>L. polyxystra</i> n. sp.	1	2	36	82	30	2	153	10.9	0.77																
Species	Ocular pectoral-fin rays										n	x	SD												
	9	10	11	12	13																				
<i>L. bilineata</i>		5	12	69	32	5	123	11.2	0.81																
<i>L. mochigarei</i>			5	14	7	1	27	11.1	0.77																
<i>L. polyxystra</i> n. sp.		5	47	74	25	2	153	10.8	0.79																

line (Table 6), and ocular-side suborbital pores (Table 7). *Lepidopsetta polyxystra* n. sp. also differed from *L. bilineata* in number of gill rakers of the upper and lower first arch and lower second arch (Table 3), dorsal-fin rays (Table 4), ocular-side and blind-side pectoral-fin rays (Table 4), anterior ADB pores (Table 5), blind-side suborbital pores (Table 7), and supraorbital pores (Table 7), and differed from *L. mochigarei* in number of gill rakers of the upper and lower first arch and lower second arch (Table 3), blind-side pectoral-fin rays (Table 4), anterior and posterior ADB pores (Table 5), and cheek scales (Table 6).

All three species were found to differ significantly in the means of two morphometric characters with either ANOVA or ANCOVA: interorbital width and ocular-side mandible length (Table 8). *Lepidopsetta polyxystra* n. sp. also differed from *L. bilineata* in seven additional characters: head length, blind-side maxilla length, cheek length, body depth, ocular-side pectoral-fin length, caudal-fin length, and caudal peduncle depth; and differed in medians in ocular-side maxilla length, blind-side pectoral-fin length, and body depth. *Lepidopsetta polyxystra* n. sp. also differed from *L. mochigarei* in means of two characters: dorsal orbit length and cheek length; and in medians of head length,

body depth, depth at caudal base, and caudal length. *Lepidopsetta bilineata* also differed from *L. mochigarei* in means of two additional characters: blind-side maxilla length and dorsal orbit length; and differed in medians in head length, ocular-side maxilla length, cheek length, body depth, caudal peduncle depth, and depth at caudal base. No differences in means were found in snout length or ocular-side maxilla length.

In the standard PCA of all three species together, loadings of morphometric PC1 were all positive and thus exhibited a strong size effect (Table 9), accounting for 95% of morphometric variation. Principal components 2 and 3 accounted for 56% of the remaining morphometric variation. Principal component 2 loadings described a gradient based on interorbital width and dorsal orbit length; PC3 loadings, a gradient on caudal peduncle depth, cheek depth, caudal depth at hypural margins, and body depth. The plot of PC2 versus PC3 revealed extensive overlap in morphometric characters (Fig. 2A). Principal components 1 and 2 of the meristics analysis accounted for 46% of the meristic variance: PC1 strongly loaded on lateral line pores and scales above and below the lateral line, preopercle pores, and suborbital pores, whereas PC2 strongly

Table 6
Counts of total scales above and below lateral line, scales above lateral line, and cheek scales for species of *Lepidopsetta*.

Species	Total body scales																												n	x	SD		
	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88									
<i>L. bilineata</i>	2	1	2	5	3	2	4	2	4	7	5	3	9	6	3	7	4	4	1	5	3	1	1	1	1								
<i>L. mochigarei</i>																																	
<i>L. polyxystra</i> n. sp.	1		1	1	1	3	1	3	6	6	4	5	5	9	10	3	7	7	3	1	3	1	3	1									
Total body scales (cont'd)																																	
	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	n	x	SD										
<i>L. bilineata</i>																					85	76.3	5.59										
<i>L. mochigarei</i>			1	1	1		1	5	2	3	1	3	3	2	1	1	1	1	1	1	27	100.1	4.42										
<i>L. polyxystra</i> n. sp.	5	2	2	2	1		1														94	80.8	5.95										
Scales above lateral line																																	
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	n	x	SD									
<i>L. bilineata</i>	1	5	8	5	8	8	13	12	9	6	4	4			1			1	1			85	31.0	3.13									
<i>L. mochigarei</i>											1	3	4	2	6	4	4	1	1	1	1	27	39.9	2.49									
<i>L. polyxystra</i> n. sp.			5	5	5	11	9	16	17	7	9	6	2	1	1							94	32.2	2.69									
Scales below lateral line																																	
	32	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	58	59	60	61	62	63	64	65	67	n	x	SD	
<i>L. bilineata</i>	1	1	1	3	10	5	6	5	9	11	10	7	6	3	3	2	2														85	45.3	3.74
<i>L. mochigarei</i>																1		1												27	60.2	3.33	
<i>L. polyxystra</i> n. sp.	1		2	1	3	1	2	7	7	15	5	12	11	11	4	2	1	2	5	1	1									94	48.6	3.95	
Cheek scales																																	
	7	8	9	10	11	12	13	14	15	16	n	x	SD																				
<i>L. bilineata</i>																																	
<i>L. mochigarei</i>			7	14	18	21	15	6	2	1	84	11.6	1.55																				
<i>L. polyxystra</i> n. sp.				2	8	9	7	1			27	11.9	1.11																				
	3	5	14	36	29	10	2				99	10.2	1.21																				

Table 7
Counts of ocular- and blind-side suborbital pores, preopercle pores, and supraorbital pores for species of *Lepidopssetta*.

Species	Ocular-side suborbital pores																																						x	SD
	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	n													
<i>L. bilineata</i>				1		1		9	8	7	16	15	2	3	6		2	1	1										72	21.2	2.71									
<i>L. mochigarei</i>											1			1			2	8	3		2	3	3		1		2	1	27	30.7	3.51									
<i>L. polyxystra</i> n. sp.	1		2		2	4	2	7	11	11	17	10	11	6	3	3	3												93	22.7	3.10									

Species	Blind-side suborbital pores																				x	SD
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	n						
<i>L. bilineata</i>	1	2	12	24	21	9	3	2								74	9.5	1.32				
<i>L. mochigarei</i>				2	3	7	8	4	2							1	27	12.9	1.94			
<i>L. polyxystra</i> n. sp.			5	17	32	31	3	4	1							93	10.3	1.16				

Species	Supraorbital pores													x	SD
	1	2	3	4	5	6	7	8	9	n					
<i>L. bilineata</i>		2	6	20	70	91	51	10	5	255	5.8	1.19			
<i>L. mochigarei</i>	17	1	1							19	1.2	0.50			
<i>L. polyxystra</i> n. sp.	118	105	29	7	2	3	2			266	1.8	1.03			

Species	Preopercle pores													x	SD
	5	6	7	8	9	10	11	12	13	n					
<i>L. bilineata</i>	2	60	9							71	11.6	1.55			
<i>L. mochigarei</i>			1	4	2	8	6	1	2	24	11.9	1.11			
<i>L. polyxystra</i> n. sp.	1	32	53	3						89	10.2	1.21			

Table 8

Proportional morphometrics of adults of *Lepidopsetta*. HL = head length; SL = standard length. Data are in hundreds of SL or HL with mean $\pm$ standard deviation (range). Statistical significance was evaluated by ANOVA and ANCOVA, when appropriate, at 0.05 level. All = Differences between all three species were significant; bp = Differences between *L. bilineata* and *L. polyxystra* n. sp. were significant; pm = Differences between *L. polyxystra* n. sp. and *L. mochigarei* were significant; ns = No significant differences were found.

	Species			Significance	
	<i>L. bilineata</i>	<i>L. mochigarei</i>	<i>L. polyxystra</i>	ANOVA	ANCOVA
Sample size	83	26	94		
Head length/SL	28.20 $\pm$ 1.64 (24.01–32.86)	26.23 $\pm$ 1.71 (23.23–30.54)	27.24 $\pm$ 1.62 (21.75–31.54)	bp	
Snout length/HL	16.09 $\pm$ 2.07 (12.37–22.45)	16.13 $\pm$ 1.69 (12.72–20.21)	16.02 $\pm$ 1.84 (12.06–20.12)	ns	ns
Ocular-side maxilla length/HL	27.88 $\pm$ 1.25 (25.26–32.53)	27.21 $\pm$ 1.41 (24.63–29.41)	26.30 $\pm$ 1.89 (20.42–31.47)	ns	
Ocular-side mandible length/HL	41.91 $\pm$ 1.69 (38.33–46.10)	39.61 $\pm$ 1.83 (36.57–44.64)	40.73 $\pm$ 2.20 (34.39–50.00)	bm	All
Interorbital width/HL	3.54 $\pm$ 0.79 (2.14–6.02)	2.68 $\pm$ 0.69 (1.32–4.17)	4.35 $\pm$ 0.80 (2.49–6.56)	All	All
Dorsal orbit length/HL	28.06 $\pm$ 1.91 (23.38–32.46)	30.08 $\pm$ 1.83 (26.09–34.74)	28.13 $\pm$ 1.95 (22.18–32.86)	pm/bm	
Ventral orbit length/HL	3.54 $\pm$ 0.79 (2.14–6.02)	2.68 $\pm$ 0.69 (1.32–4.17)	4.35 $\pm$ 0.80 (2.49–6.56)		
Cheek length/HL	34.17 $\pm$ 2.84 (28.06–41.84)	31.09 $\pm$ 1.71 (28.57–34.98)	32.54 $\pm$ 2.77 (26.67–38.52)	bp/pm	
Body depth/SL	46.98 $\pm$ 2.84 (40.80–57.04)	51.79 $\pm$ 3.23 (45.54–61.04)	49.02 $\pm$ 3.44 (41.17–58.93)	bp	
Ocular-side pectoral length/SL	15.19 $\pm$ 1.34 (12.20–18.20)	14.58 $\pm$ 1.24 (12.60–17.42)	14.66 $\pm$ 1.52 (10.73–18.23)	bp	
Caudal-fin length/SL	20.79 $\pm$ 1.57 (17.62–23.63)	21.22 $\pm$ 1.69 (18.77–25.14)	22.72 $\pm$ 1.77 (17.78–29.13)	bp	
Caudal peduncle depth/SL	10.20 $\pm$ 0.80 (8.18–12.29)	11.03 $\pm$ 0.94 (9.71–13.96)	10.91 $\pm$ 0.71 (9.36–13.13)	bp	
Caudal peduncle length/SL	9.11 $\pm$ 0.72 (7.18–10.87)	8.89 $\pm$ 0.54 (7.77–10.28)	8.90 $\pm$ 0.62 (7.01–10.12)		
Ocular-side pelvic length/SL	9.83 $\pm$ 0.98 (7.64–12.50)	9.82 $\pm$ 0.94 (7.40–11.75)	9.95 $\pm$ 0.97 (7.84–12.15)		
Sample size	77	26	93		
Blind-side maxilla length	31.26 $\pm$ 2.25 (25.16–41.18)	29.73 $\pm$ 1.56 (27.30–32.87)	28.70 $\pm$ 2.01 (22.22–35.66)	bp/bm	bp/bm
Sample size	78	26	93		
Blind-side pectoral length/SL	9.91 $\pm$ 0.77 (7.33–12.22)	9.58 $\pm$ 0.90 (7.89–11.69)	10.16 $\pm$ 1.17 (6.58–12.66)		
Sample size	67	26	92		
Cheek depth/HL	19.15 $\pm$ 2.13 (13.92–24.19)	19.64 $\pm$ 2.60 (14.83–25.53)	18.62 $\pm$ 2.17 (13.56–22.73)		
Caudal depth at hypurals/SL	12.13 $\pm$ 0.69 (10.46–14.25)	13.12 $\pm$ 0.70 (11.66–14.61)	12.35 $\pm$ 0.88 (10.06–16.91)		
Sample size	8	6	15		
Lateral line length/lateral line depth	30.20 $\pm$ 3.78 (24.84–37.06)	33.42 $\pm$ 3.78 (27.86–38.98)	31.72 $\pm$ 3.41 (26.29–38.20)		

Table 9

Character loadings for principal component analysis of morphometric characters of adult *Lepidopsetta bilineata*, *L. mochigarei*, and *L. polyxystra* n. sp.

Characters	Loadings		
	PC1	PC2	PC3
Standard length	0.22484	0.06236	0.15282
Head length	0.22819	0.03318	-0.06512
Snout length	0.21789	0.00863	-0.04715
Ocular-side maxilla length	0.23138	0.05417	-0.30392
Blind-side maxilla length	0.23849	0.0835	-0.30268
Ocular-side mandible length	0.2334	0.03438	-0.20318
Dorsal orbit length	0.21415	0.11385	-0.09032
Ventral eye length	0.20185	0.09275	-0.20682
Interorbital width	0.22077	-0.96363	-0.03502
Cheek length	0.24796	0.00482	-0.13585
Cheek depth	0.25623	0.08324	-0.39732
Body depth	0.23716	0.08671	0.33759
Ocular-side pectoral length	0.24489	0.0723	-0.01453
Blind-side pectoral length	0.24277	0.01015	0.184878
Ocular-side pelvic length	0.22725	0.0275	0.076978
Caudal peduncle length	0.22574	0.08882	0.121448
Caudal peduncle depth	0.22183	0.00716	0.401018
Caudal depth at hypurals	0.22707	0.07164	0.377584
Caudal-fin length	0.20981	-0.00818	0.20981

loaded on gill rakers of the lower first and second arches and upper first arch and supraorbital pores (Table 10). By plotting PC1 of the meristic analysis and PC2 of the morphometric analysis (Fig. 2C), we found a distinct cluster representing *L. mochigarei* and an overlap of clusters representing *L. bilineata* and *L. polyxystra* n. sp.

In the PCA of only the eastern North Pacific species, loadings of morphometric PC1 were all positive and thus exhibited a strong size effect, accounting for 96% of morphometric variation. Principal components 2 and 3 accounted for 33% and 19% of the remaining morphometric variation, respectively. Principal component 2 loadings described a gradient based primarily on interorbital width, as well as on ventral orbit length and blind-side maxilla length; PC3 loadings described a gradient on interorbital width, caudal peduncle depth, and body depth. The plot of PC2 versus PC3 revealed extensive overlap in morphometric characters (Fig. 3A). Principal components 1 and 2 of the meristic analysis accounted for 28% and 17%, respectively, of the meristic variance: PC1 strongly loaded on gill rakers and supraorbital pores and PC2 strongly loaded on dorsal-fin rays, anal-fin rays, and cheek scales. The plot of meristic PC1 versus PC2 revealed two distinct clusters (Fig. 3B). By plotting PC1 of the meristic analysis and PC2 of the morphometric analysis (Fig. 3C), we found two distinct clusters representing *L. bilineata* and *L. polyxystra* n. sp.

Table 10

Character loadings for principal component analysis of meristic characters for *Lepidopsetta bilineata*, *L. mochigarei*, and *L. polyxystra* n. sp. ADB = supratemporal branch of the lateral line.

Characters	Loadings	
	PC1	PC2
Upper 1 st arch gill rakers	0.0722	0.4021
Lower 1 st arch gill rakers	0.0646	0.4414
Upper 2 nd arch gill rakers	0.0067	0.1393
Lower 2 nd arch gill rakers	0.0181	0.406
Dorsal-fin rays	-0.1314	-0.1926
Anal-fin rays	-0.1265	-0.1939
Ocular-side pectoral-fin rays	-0.0975	-0.1331
Blind-side pectoral-fin rays	-0.0759	-0.1527
Lateral-line pores	-0.4017	0.1027
ADB1 pores	0.2092	0.1578
ADB2 pores	0.0079	0.1962
Interorbital scales	-0.0508	0.2163
Cheek scales	-0.1907	-0.2532
Scales above lateral line	-0.384	0.0291
Scales below lateral line	-0.392	0.0873
Ocular-side suborbital pores	-0.3635	0.0177
Blind-side suborbital pores	-0.3007	0.0961
Preopercle pores	-0.3643	0.0394
Supraorbital pores	0.203	-0.3731

When data points of eastern North Pacific species were identified by geographic regions, no significant clustering was apparent within groups of either *L. bilineata* or *L. polyxystra* n. sp. Extensive overlap was found between clusters representing each of these general geographic areas.

Larvae

Raw morphometric data were subjected to an ANCOVA analysis, which indicated differences in several morphological characters (snout-to-anus length, body depth, and orbit length) between larvae of *L. bilineata* and *L. polyxystra* n. sp. at various stages of development (Table 11). Several characters showed significant differences in post-flexion larvae ($P < 0.0001$), including snout-to-anus length, head length, and orbit length. Snout-to-anus length is shorter in larvae of *L. bilineata* during the preflexion, flexion, and postflexion stages (Fig. 4). Larvae of *L. bilineata* are deeper-bodied during the yolk sac, preflexion, and flexion stages of development (Fig. 5). The PCA plots of PC2 and PC3 for each developmental stage produced broadly overlapping clusters.

Systematics

Genus *Lepidopsetta* Gill, 1862

Lepidopsetta Gill, 1862:330 (type species *Platichthys umbrosus* Girard, 1856 [originally cited as *Psettichthys umbrosus* but subsequently corrected by Gill (1864)], by monotypy).

Diagnosis

Pleuronectid genus *Lepidopsetta* is distinguished by the following combination of characters in adults: lateral line with a high arch, 6–8 scale rows between highest point of arch and base of arch over the pectoral fin; supratemporal branch of lateral line with a moderately elongate posterior extension of up to 35 pored scales; mouth small, maxilla extending to anterior quarter of ventral orbit; expanded anteriormost anal pterygiophore ("anal spine") present, often projecting beyond body wall in damaged specimens; supraorbital pores present; scales on ocular side often tuberculate, especially on the head and anterior portion of body; scales on blind side always cycloid anteriorly.

Larvae are distinguished from other pleuronectid genera by the following combination of characters: dorsal and anal finfold pigment present, 1–3 postanal bars (2–4 distinctive pigment regions along dorsal midline), a series of ventral midline melanophores, absence of slashlike hypaxial pigment along the postanal body, few to many pigment spots around the notochord tip, and 37–44 total myomeres (Table 12).

Description of adults

Body ovate, greatest depth 31.7–61.0% SL, scales above lateral line 25–45, scales below lateral line 27–67; head acute to rounded, length 21.8–32.9% SL; dorsal margin of head concave to nearly linear, snout length 3.1–6.2% SL (12.1–22.4% HL); mouth small, premaxilla with fleshy lips and prominent, broad-based posterior lobe, maxilla extending to anterior rim of ventral orbit, ocular-side maxilla shorter than blind-side maxilla, ocular-side maxilla length 20.4–32.5% HL, blind-side maxilla length 22.2–41.2% HL; ocular-side mandible length 34.4–50.0% HL, about equal in length to blind-side mandible; teeth conical and slightly lobate or truncate, largest are anterior becoming gradually smaller posteriorly, fewer on ocular-side premaxilla and dentary, 4–10 on ocular-side premaxilla, 20–27 on blind-side premaxilla, 8–15 on ocular-side dentary, 20–29 on blind-side dentary; gill rakers of first arch moderately slender to broad and robust, 6–14 total, 1–6 on upper and 4–9 on lower arch; gill rakers of second arch broad and robust, 6–14 total, 0–4 on upper and 5–13 on lower arch; dorsal orbit round (nearly equal to eye length) to elliptical (posterior rim elongate and much greater than eye length), orbit length 22.2–34.7% HL,

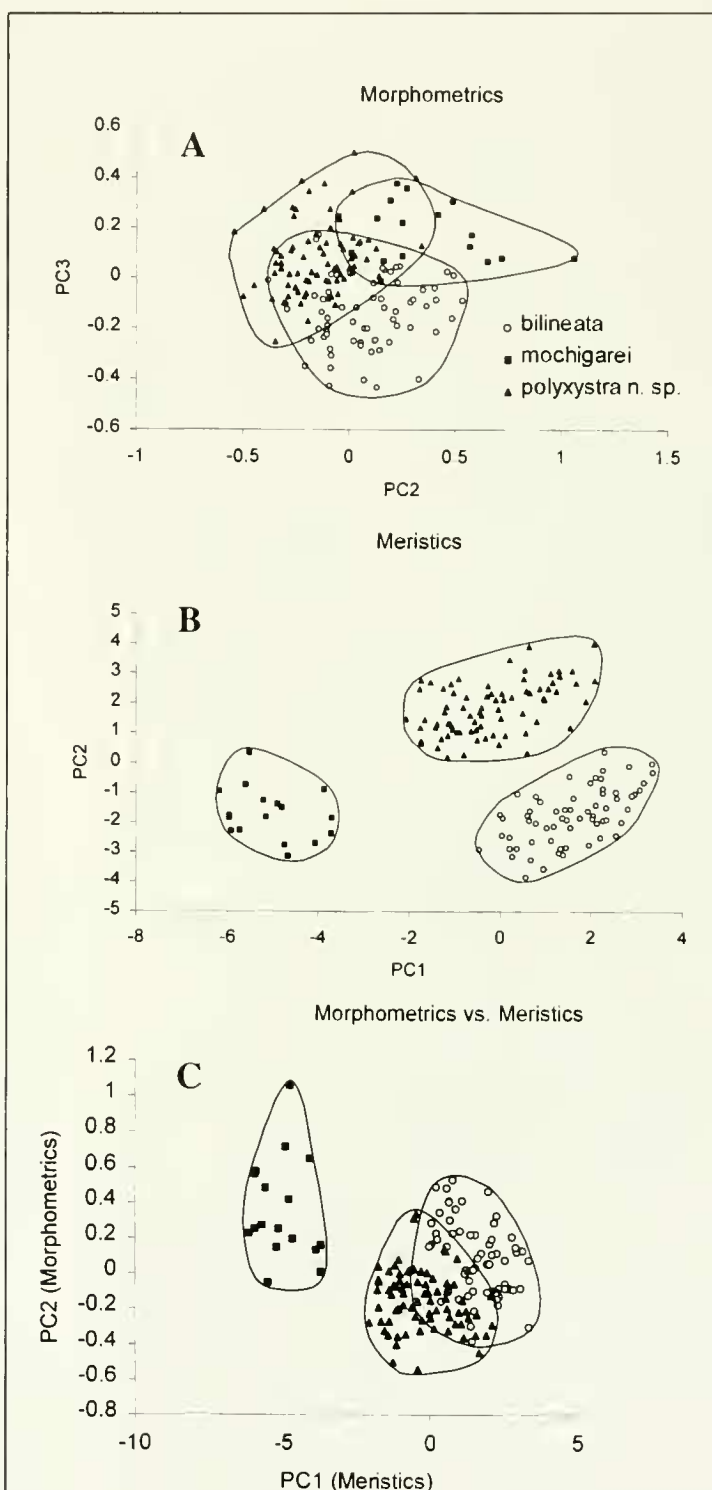
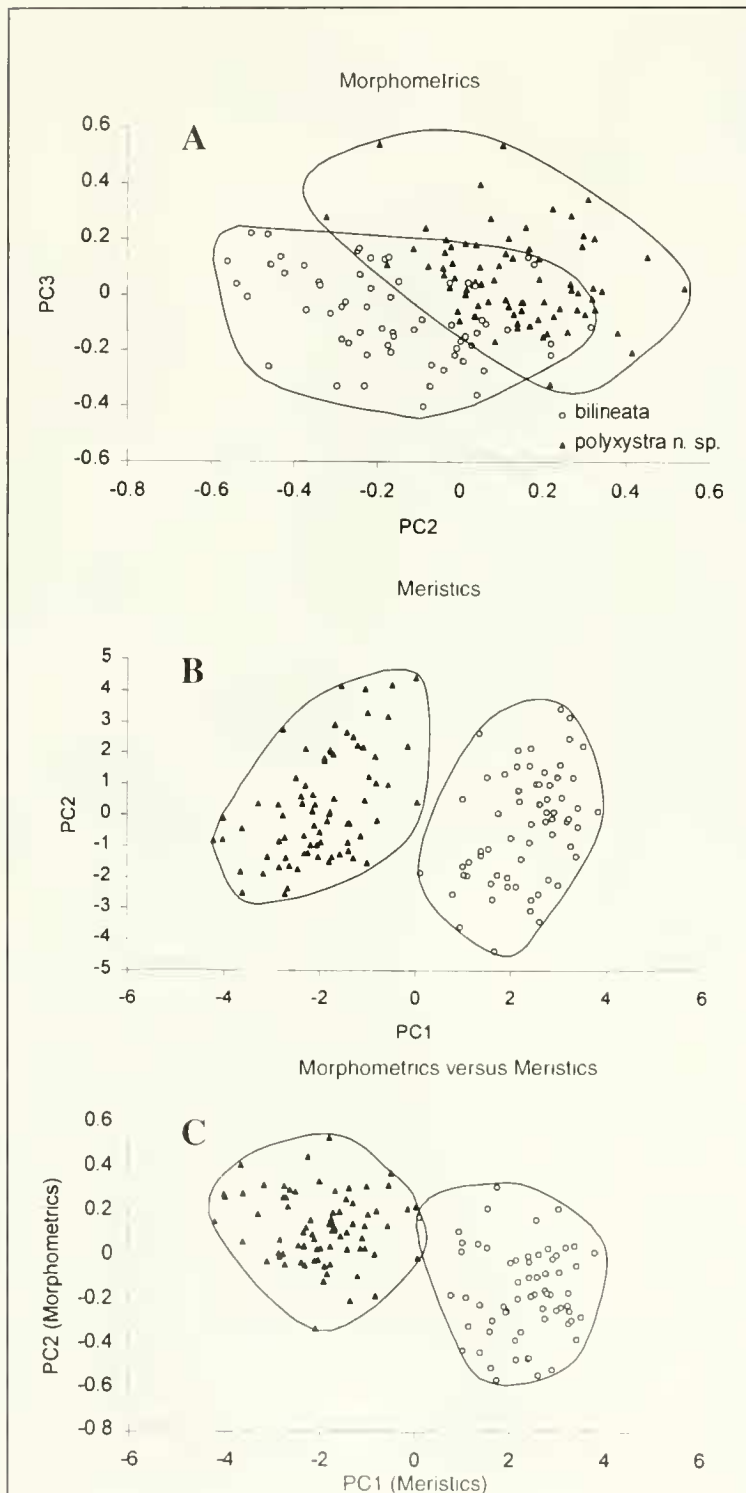
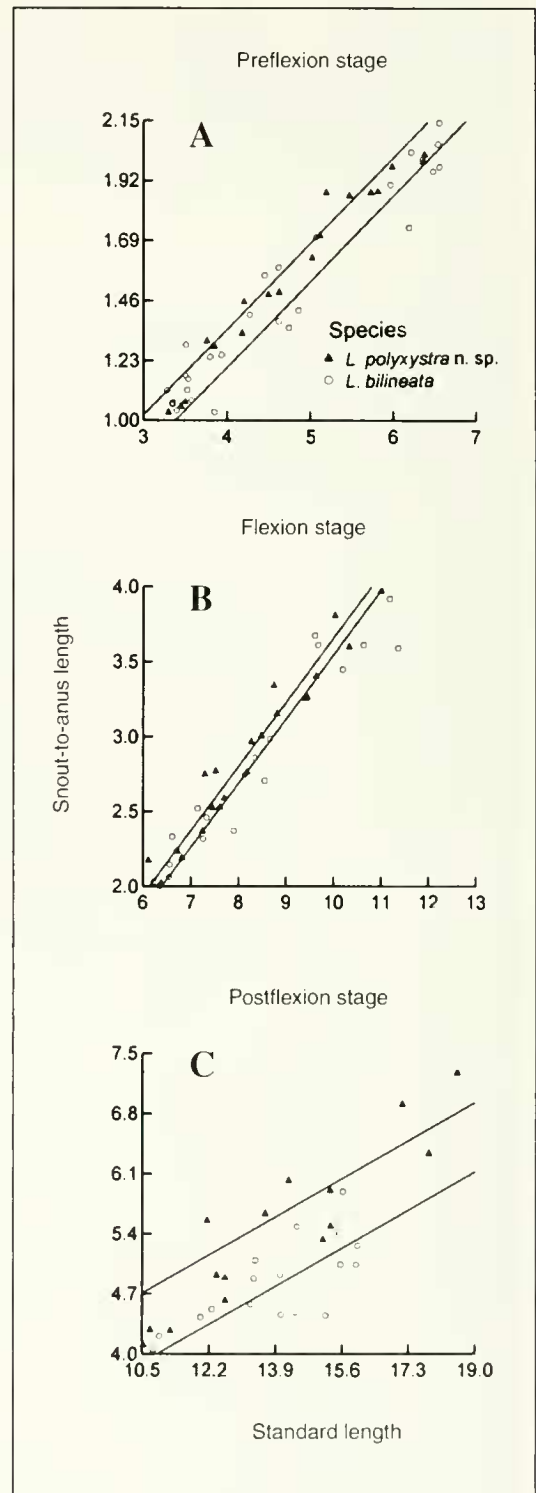


Figure 2

Plots of principal component scores for morphometric and meristic characters for *Lepidopsetta* species: *L. bilineata* (circle), *L. mochigarei* (square), *L. polyxystra* n. sp. (triangle). (A) Morphometric characters only; (B) meristic characters only; (C) morphometric characters (PC2) versus meristic characters (PC1).

**Figure 3**

Plots of principal component scores for morphometric and meristic characters for eastern North Pacific *Lepidopsetta* species: *L. bilineata* (circle), *L. polyxystra* n. sp. (triangle). (A) Morphometric characters only; (B) meristic characters only; (C) morphometric characters (PC2) versus meristic characters (PC1).

**Figure 4**

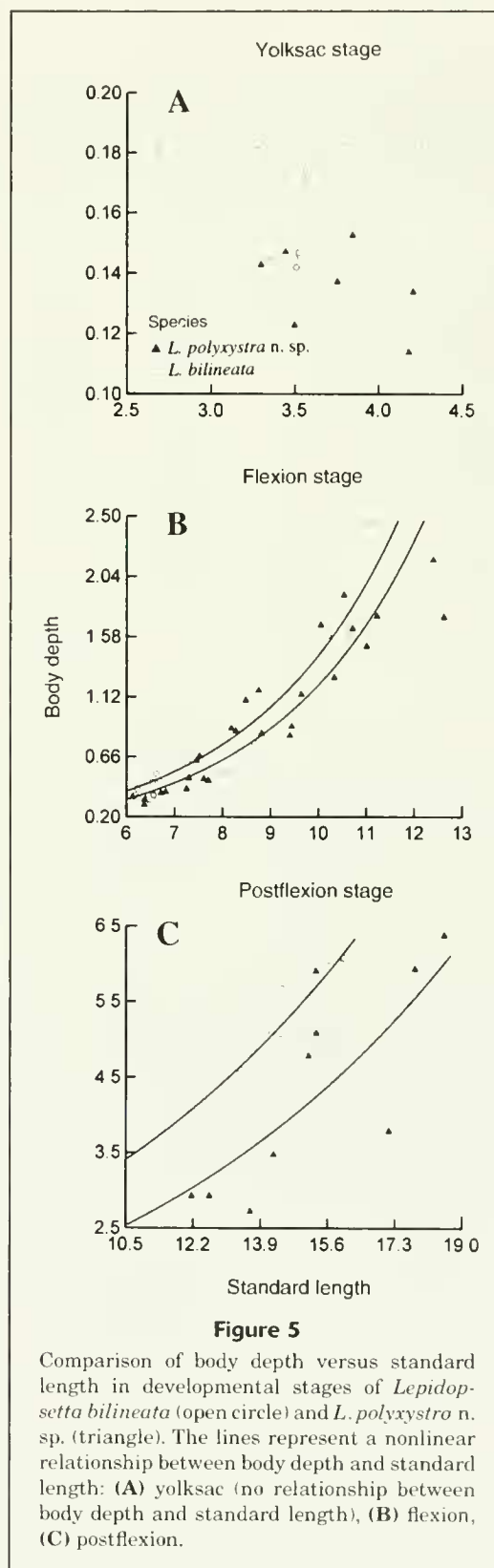
Comparison of snout-to-anus length versus standard length in developmental stages of *Lepidopsetta bilineata* (open circle) and *L. polyxystra* n. sp. (triangle). The lines represent a linear regression with both species having similar slopes: (A) preflexion, (B) flexion, (C) postflexion.

Table 11

P-values for ANCOVA of larvae of *Lepidopsetta bilineata* and *L. polyxystra* n. sp. Bold values indicate that the species are different from each other at the 0.05 significance level.

Character	Stage of development			
	Yolksac	Preflexion	Flexion	Postflexion
Snout-to-anus length	NS	<i>P</i>=0.001	<i>P</i>=0.035	<i>P</i><0.001
Body depth	<i>P</i>=0.001	NS	<i>P</i>=0.037	<i>P</i><0.001
Head length	NS	NS	NS	<i>P</i>=0.001
Snout length	NS	NS	NS	NS
Orbit length	NS	<i>P</i>=0.020	NS	<i>P</i><0.001

dorsal eye length 17.9–32.9% HL; ventral eye approximately equal in length to ventral orbit, length 17.2–35.4% HL; interorbital with up to 5 scales (often lost in preserved material), width 1.3–6.6% HL; cheek with 7–16 scales, length 26.7–65.9% HL, depth 13.6–33.6% HL; preopercular pores 5–13; ocular-side suborbital pores 13–38; blind-side suborbital pores 6–20; lateral line with a high arch, 6–8 scale rows high over the pectoral fin, arch length about three times its depth, length 26.1–69.9% HL, lateral line pores 70–119; anterior supratemporal short, pores 2–15; posterior supratemporal branch moderately elongate, pores 6–35; supraorbital canal short or long, pores 1–9; pectoral fins with 8–13 rays, dorsal 2–3, and ventralmost simple and all others branched, ocular-side pectoral fin longer than blind-side pectoral fin, length 10.7–18.2% SL (38.3–70.4% HL), blind-side pectoral fin about equal in length to pelvic fins, length 6.6–12.7% SL (23.2–49.6% HL); pelvic fins with 6 branched rays, ocular-side pelvic-fin length about equal to blind-side pelvic-fin length, 7.4–12.5% SL (26.7–45.9% HL); dorsal-fin origin over anterior portion of dorsal orbit, dorsal fin with 64–89 simple soft rays, smallest rays anterior and posterior, longest rays at midbody, height 10.2–16.6% SL; dorsal-fin pterygiophores 68–78 in specimens with 64–83 dorsal-fin rays, 8–11 anterior to first neural spine, the first bifurcate and supporting two rays; anal fin with 49–77 simple soft rays in specimens with 54–63 anal-fin rays supported by 53–63 pterygiophores, fin about equal in height to dorsal fin; anal-fin rays 1 and 2 supported by greatly expanded anterior pterygiophore, sharp point of which often projects through skin between anal-fin origin and anus; caudal peduncle length 7.0–10.9% SL (25.5–42.2% HL); least caudal peduncle depth 8.2–14.0% SL (29.6–50.3% HL; 90.0–172.0% caudal peduncle length); greatest caudal peduncle depth 10.1–16.9% SL (37.2–57.7% HL); caudal fin truncate to rounded, with 18–19 rays, total of 8–10 both dorsally and ventrally, five on each of complex hypurals 1+2 and 3+4, 3 on hypural 5, one on the epural or preural 2 neural spine, and four on the parhypural, length 15.3–29.1% SL; vertebrae 39–42, 11 precaudal and 28–31 caudal, neural spines 1–3 and haemal spines 1–4 anteroposteriorly



expanded, epineurals present on vertebrae 2–11, ribs present on vertebrae 3–11. Meristics are summarized in Tables 3–7.

Table 12

Summary of selected larval characters helpful in distinguishing eastern North Pacific pleuronectid larvae during preflexion and early flexion stages (Matarese et al., 1989, in part). Characters are presented for taxa where at least some early life-history stages are known. Only general trends are presented because pigment may vary among specimens. When specimens were not available, subjective decisions were based on previously published material. PVM = postventral melanophores.

Genus	Pigment characters							Total myomeres
	Postanal bars	Hypaxial	PVM	Notochord tip	Dorsal finfold	Anal finfold	Head spines	
<i>Embassichthys</i>	3	Absent	Absent	Present	Present	Present	Absent	57–65
<i>Eopsetta</i>	3	Absent	Absent	Present	Absent	Absent	Preopercular	41–45
<i>Glyptocephalus</i>	4	Absent	Absent	Present	Present/ absent	Present/ absent	Preopercular	52–66
<i>Hippoglossoides</i>	3–4	Present	Absent	Present	Present	Present	Absent	44–51
<i>Isopsetta</i>	3	Absent	Absent	Present	Absent	Present	Absent	41–42
<i>Lepidopsetta</i>	1–3	Absent	Present	Present	Present	Present	Absent	37–44
<i>Microstomus</i>	3–4	Absent	Absent	Present	Present	Present	Otic	50–55
<i>Psettichthys</i>	1	Absent	Absent	Present	Present	Present	Absent	38–41
<i>Acanthopsetta</i>	Absent	Present	Present	Present	Absent	Absent	Absent	39–40
<i>Atheresethes</i>	Absent	Absent	Absent	Present/ absent	Absent	Absent	Preopercular/ supraocular crest	47–50
<i>Hippoglossus</i>	Absent	Present	Absent	Present	Present	Present	Absent	49–51
<i>Limanda</i>	Absent	Present	Present	Absent	Absent	Present	Absent	40–41
<i>Liopsetta</i>	Absent	Absent	Absent	Present	Absent	Absent	Absent	37–41
<i>Lyopsetta</i>	Absent	Present	Absent	Present	Present	Present	Absent	43–47
<i>Parophrys</i>	Absent	Present	Present	Present	Absent	Present	Absent	42–47
<i>Plotichthys</i>	Absent	Absent	Present	Present	Present	Present	Absent	35–38
<i>Pleuronectes</i>	Absent	Absent	Present	Absent	Absent	Present	Absent	41–42
<i>Pleuronichthys</i>	Absent	Absent	Absent	Present	Present	Present	Absent/otic	38–41
<i>Reinhardtius</i>	Absent	Present	Absent	Present	Present	Present	Absent	61–64

Ocular-side scales ctenoid, often tuberculate, especially on anterior portion of the body around the head and pectoral girdle; tubercles columnar, narrow from base to tip, up to 10 tubercles on scales of head, fewer on tuberculate body scales; blind-side scales nearly always cycloid except in ambicolored specimens, never tuberculate, posterior scales occasionally with central cteni along lateral midline; broad, flaplike urogenital pore on ocular side, dorsal to anus; anus just anterior to anal-fin origin; color of ocular side varies with substrate, in life olivaceous greenish brown with various blotches of dark brown and spots of light areas scattered over body, brown streaks in dorsal, anal, and caudal fins, often with a series of four to five large light spots at base of dorsal fin and four similar spots at base of anal fin; in preservation ocular side yellowish brown with blotches; blind side bright white to cream in life, cream to yellowish in preservation. Moderate sized pleuronectids, reaching a standard length of 600 mm (Hart, 1973).

Description of larvae

Snout-to-anus length remaining constant during development, length 32.1–39.3% SL; preflexion body slender, body depth increasing with development, sharply after

flexion, from a depth of 3.8 to 35.7% SL; finfolds of moderate size; head length increasing with development, sharply after flexion, from a length of 11.6 to 29.3% SL; snout length remaining constant during development, length 20.5–24.7% HL; orbit length decreasing with development, from 51.9 to 20.9% HL.

Size at stage of development variable among species (Table 13). Larvae hatching at less than 3.0–4.45 mm; yolk absorbed by 2.7–4.5 mm. Preflexion larvae ranging in size from 3.8 to 6.6 mm; flexion larvae between 6.4 and 11.1 mm; postflexion larvae between 10.8 and 18.6 mm. Transformation occurring at sizes as small as 10.0 mm; juvenile stage usually attained by 35.0 mm (Table 13).

Preanal pigment present initially along lower jaw, increasing posteriorly with development. Pigment occurring ventrally along gut and dorsally on anus; by flexion a distinct patch of melanophores occurring along the posterior edge of the gut, with pigment increasing laterally with development. Pigment may be present or absent on pectoral-fin rays and base.

Postanal pigment in preflexion larvae may be present as melanophores along distal edges of dorsal and anal finfolds, but typically with isolated patches along finfolds and pigment spots or patches along distal edges of anal finfold; when present, two to four distinct pigment regions along

Table 13

Length at stage of development for species of *Lepidopsetta* (mm SL). For a more complete explanation of each developmental stage, see Kendall et al. (1984).

Stage	<i>L. bilineata</i>	<i>L. mochigarei</i>	<i>L. polyxystra</i> n. sp.
Egg	~1.0	0.90	~1.0
Hatch	<3.0	3.95–4.48	>3.0
Yolk absorption	2.7–4.5	unknown	3.3–4.2
Preflexion	3.8–6.6	unknown	4.2–6.2
Flexion	6.4–11.1	~8.9–10.6	6.2–12.6
Postflexion	10.8–16.0	unknown	12.2–18.6
Transformation	as small as 10.0	as small as 15.3	as small as 15.0
Early juvenile	complete as small as 13.0 (13.0–33.9)	unknown	complete as small as 26.0
Postsettlement juvenile	<35.0	unknown	>35.0

dorsal midline; a series of melanophores present from the gut along the ventral midline posterior to anus to just posterior to ventral stripe of posteriormost bar; a few melanophores on the caudal peduncle and above and below the notochord tip.

Distribution

The genus is endemic to the North Pacific and is widespread on the continental shelf (Figs. 6–13). Its range extends from Yongil Bay, Korea, in the southern Sea of Japan and along the northern coasts of Japan, north through the Sea of Okhotsk and the Bering Sea, the most northerly record being from the Gulf of Anadyr and the vicinity of St. Lawrence Island. It is recorded from the Aleutian Islands and into the eastern North Pacific throughout the Gulf of Alaska, south into Puget Sound and along the west coast of Washington, Oregon, California, and Mexico. Its most southerly record in the eastern Pacific is from the Cortez Banks of Baja California, Mexico.

Larvae of the eastern North Pacific species range from the Bering Sea and Aleutian Islands along the Pacific coast to Baja California (Figs. 12–13). Both species co-occur in the eastern Aleutian Islands to the Washington coast; only larvae of *L. polyxystra* n. sp. have been routinely collected from the Bering Sea and only larvae of *L. bilineata* have been collected from California and south in California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples. A subset of larvae collected by AFSC surveys in the Gulf of Alaska and Bering Sea was examined to compare differences in temporal distribution and mean density (number/10 m²; Appendix Table 1). During the 22-year sampling period, larvae of *L. polyxystra* n. sp. appear first in our March collections (Table 14), whereas larvae of *L. bilineata* first appear in April. The largest catches of *L. polyxystra* n. sp. occurred in May, whereas the largest catches of *L. bilineata* occurred in June. Overall, in the subset of cruises from 1972 to 1994 considered in our study, *L. polyxystra* n. sp. were more abundant and mean

density was higher (5.34/10 m²) than that of *L. bilineata* (0.414/10 m²).

Habitat

Species of the continental shelf were collected over sand and gravel, commonly at depths of 200 m and less, to as deep as 575 m (Allen and Smith, 1988). For eastern North Pacific species, highest densities of larvae were found over depths of less than 500 m, although they were also collected over deeper water.

Life history

Described eggs of *Lepidopsetta* are demersal, off-round, and have a sticky chorion, causing them to adhere to each other or to a substrate, and range in size from 0.86 to 1.08 mm in diameter (Yusa, 1958; Pertseva-Ostroumova, 1961; Penttilä, 1995). The reproductive season extends from winter to early summer, generally earlier in southern species, and spawning occurs at depths of less than 220 m. All sexually mature *Lepidopsetta* apparently migrate from shallow shelf areas in the fall to deeper upper slope waters during winter and migrate back into shallower shelf waters during spring and summer. Immature *Lepidopsetta* remain in shallow waters throughout the winter and migrate into shallower coastal waters in the spring and summer.

Garrison and Miller (1982) provided a summary of reproductive characteristics of *Lepidopsetta* from the western and eastern Pacific Ocean, which included *L. bilineata* and *L. polyxystra* n. sp. Blackburn (1973) described the ichthyoplankton from Skagit Bay, Washington, located in the northernmost region of Puget Sound and included descriptions and illustrations of larvae of *Lepidopsetta*. The Washington Department of Fisheries (WDF) has reported eggs of *Lepidopsetta* (*L. bilineata* or *L. polyxystra* n. sp., or both) from late December through early March in sandy gravel of upper intertidal beaches in several sites in central and

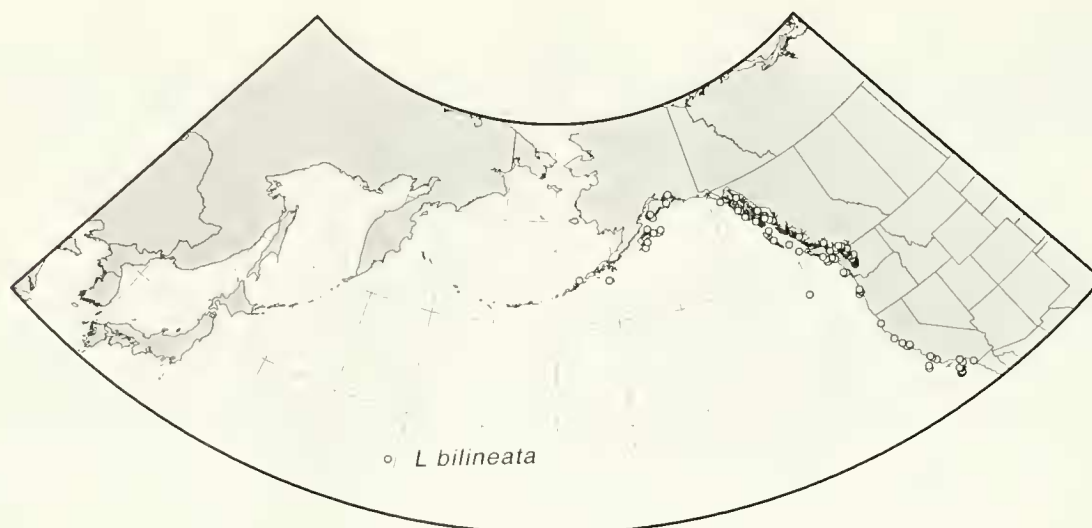


Figure 6

Distribution of adults of *Lepidopsetta bilineata* based on material examined. Each symbol may represent more than one capture.

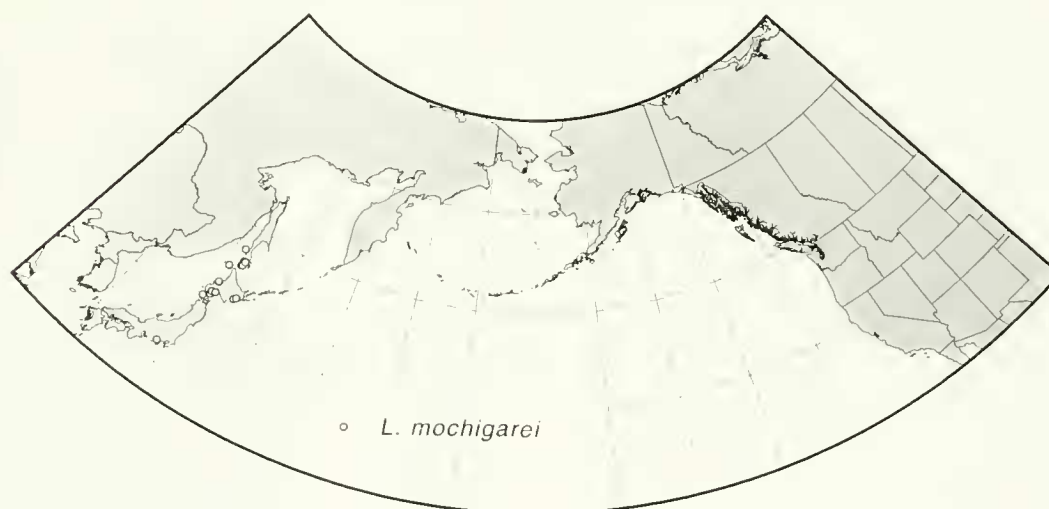


Figure 7

Distribution of adults of *Lepidopsetta mochigarei* based on material examined. Each symbol may represent more than one capture.

southern Puget Sound (Penttila, 1995). These eggs were described as demersal and adhesive ("clinging to upper beach surface material," p. 238). Eggs were collected at the same times and location as those of surf smelt (*Hypomesus pretiosus*) and Pacific sand lance (*Ammodytes hexapterus*).

Etymology

The name *Lepidopsetta* is derived from the Greek *lepidō* meaning "scaled," a probable reference to the strongly cte-

noid scales found on the ocular side of most individuals, and *psetta*, meaning "flatfish".

Comments

Sakamoto (1984a) synonymized *Lepidopsetta* (as well as five other pleuronectid genera: *Limanda*, *Parophrys*, *Isopsetta*, *Pseudopleuronectes*, and *Liopsetta*) with *Pleuronectes*, based on a phenetic analysis of detailed morphological data. Several recent authors have criticized Sakamoto's (1984a) phylogenetic techniques (Chapleau [1993]; Rass



Figure 8

Distribution of adults of *Lepidopsetta polyxystra* n. sp. based on material examined. Each symbol may represent more than one capture.

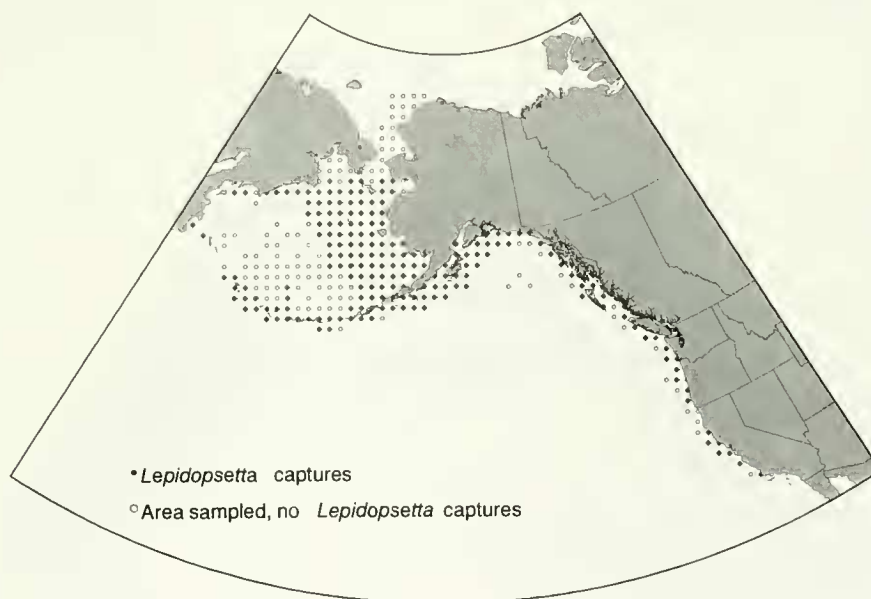


Figure 9

Records of *Lepidopsetta* from the National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering survey database 1948–1997.

[1996]; Berendzen, [1998]; Cooper and Chapleau [1998]) and have refuted the monophyly of *Pleuronectes sensu* Sakamoto (Rass [1996]; Cooper and Chapleau [1998]). Cooper and Chapleau (1998) recently conducted a cladistic analysis and resurrected these genera from synonymy with *Pleuronectes*. We follow the consensus among most current scientists (Nelson, 1994; Cooper and Chapleau,

1996, 1998; Rass, 1996) and recognize each of these genera as distinct.⁴

⁴ We do not recognize two other generic nomenclatural changes recommended by Cooper and Chapleau (1998) and have chosen to retain *Embassichthys* and *Atheresthes* as separate genera, distinct from *Microstomus* and *Reinhardtius*, respectively.

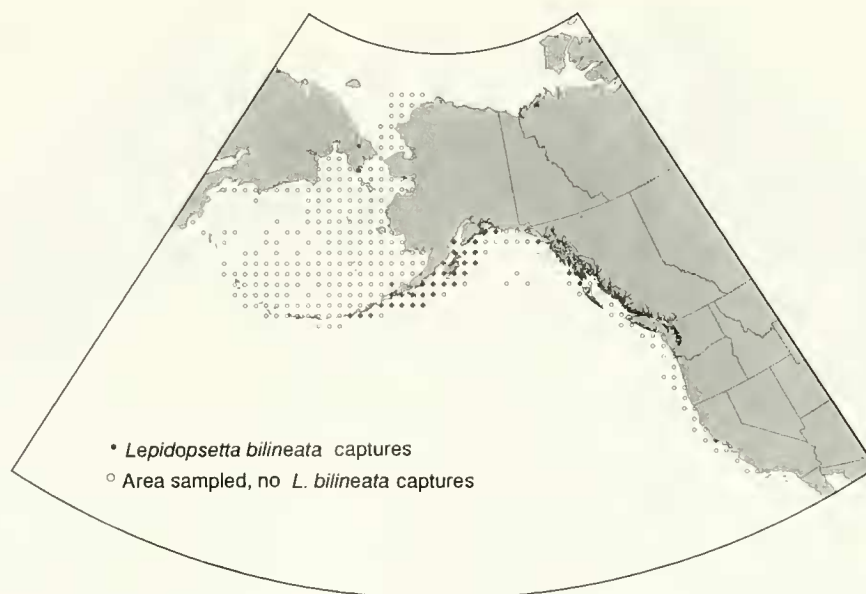


Figure 10

Records of *Lepidopsetta bilineata* from the National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering survey database, 1995–1998.

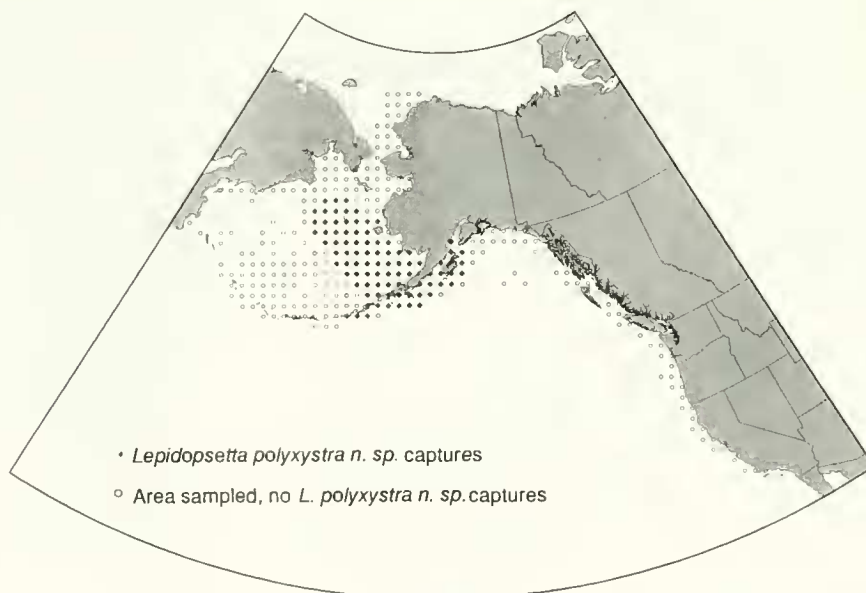


Figure 11

Records of *Lepidopsetta polyxystra* n. sp. from the National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering survey database, 1995–1998.

Supraorbital pores have not been reported in other flatfishes. The supraorbital canal is an extension of a nerve branch arising from between the frontals at the posterior rim of the dorsal orbit. In *Lepidopsetta* the pores of the canal are supported by a series of 1–6 bones (Fig. 14), sim-

ilar in size and shape to the suborbitals. Typically each bone shares in the support of one or two pores.

Among other North Pacific pleuronectids examined, *Parophrys vetulus*⁵ has 6–11 pores and *Isopsetta isolepis* 2–12 pores, whereas *Limanda aspera* and *L. pinnifasciatus*,



Figure 12

Distribution of larvae of *Lepidopsetta bilineata* based on material examined. Each symbol may represent more than one capture. Sampling effort by the National Marine Fisheries Service, Alaska Fisheries Science Center, was limited in regions between Kodiak and Vancouver Islands; other data are not available from alternate sources.



Figure 13

Distribution of larvae of *Lepidopsetta polyxystra* n. sp. based on material examined. Each symbol may represent more than one capture. Sampling effort by the National Marine Fisheries Service, Alaska Fisheries Science Center, was limited in regions between Kodiak and Vancouver Islands; other data are not available from alternate sources.

⁵ Cooper and Chapleau (1998) changed the specific epithet of *Parophrys vetulus* to *vetula* to agree in gender with *Parophrys*. However, because Girard's (1854) original description did not specify

his treatment of *vetulus* and because it may also be treated as a noun in apposition, we consider this change an incorrect subsequent spelling and retain *P. vetulus*.

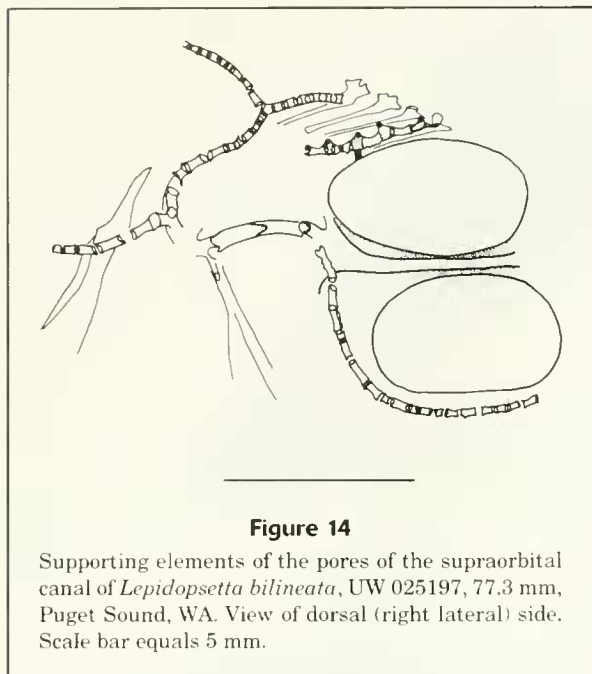


Figure 14

Supporting elements of the pores of the supraorbital canal of *Lepidapsetta bilineata*, UW 025197, 77.3 mm, Puget Sound, WA. View of dorsal (right lateral) side. Scale bar equals 5 mm.

Psettichthys melanostictus, and *Inapsetta ischyra* (a possible hybrid of *Platichthys stellatus* and *Parophrys vetulus*) have a single pore. In *Hippoglossoides elassadan* and *H. robustus*, a series of pores is found at the anterior extension of the supratemporal line, as depicted by Lindberg and Fedorov (1993) for *H. elassadan* (their Fig. 33). These pores are apparently part of the anterior extension of the trunk lateral line, but ventrally the pores extend near the dorsal orbital rim. In one specimen of *H. elassadan* examined (UW 040271), the pores extended nearly the same length along the rim of the dorsal orbit as the length for the same pores in some *L. bilineata*.

Pleuronectid larvae are difficult to diagnose on the basis of a simple set of characters. Pleuronectids are oviparous and spawn planktonic or demersal eggs (about 0.66–4.5 mm), with homogenous yolk that is either pigmented or not, and usually contains no oil. Among eastern North Pacific pleuronectids, *Lepidapsetta* is the only genus that produces demersal eggs, which are off-round and have a sticky chorion that causes them to adhere to each other or to a substrate (Pertseva-Ostroumova, 1961; Penttilä, 1995). Pleuronectid larvae hatch between 1.7 and 16.0 mm; yolk-sac and preflexion larvae are slender, becoming deeper-bodied during the postflexion stage. Larvae of *Lepidapsetta* hatch at <3.0–4.5 mm; preflexion larvae are slender and have moderate-size finfolds.

Larval pigmentation (including finfold) varies considerably in pleuronectids. A combination of pigment pattern (postanal bands, bars, and finfold), meristic characters, and size at development is needed for identification (Matarese et al., 1989; Charter and Moser, 1996). Larvae with special characters (e.g. *Atheresthes* larvae with head spines) or high myomere counts (e.g. *Embassichthys*) are easily distinguished. Other pleuronectid larvae are usually distinguished by a combination of pigmentation characters

including the number of postanal bands and bars and finfold pattern (Table 12).

No single early life history character distinguishes larvae of *Lepidapsetta* from other pleuronectid genera. Depending on developmental stage, larvae of *Lepidapsetta* generally are categorized by the presence of at least one postanal bar (Table 12). Larvae of *L. bilineata* have a postanal pigment pattern with four dorsal pigment patches (the posteriormost aligning with a ventral patch forming a caudal bar), larvae of *L. machigarei* have three dorsal patches (the posteriormost aligns with a ventral pigment patch approximating a caudal bar), whereas larvae of *L. polyxystra* n. sp. have two dorsal pigment patches (the posteriormost aligns with a ventral pigment patch forming a bar located at about 2/3 of body length). Among other pleuronectid genera that have a postanal band and bar pattern, preflexion and early flexion larvae of *Lepidapsetta* may be distinguished by the presence of a series of postanal ventral midline melanophores and fewer pigment spots along the notochord tip (Table 12).

In general, larvae of *L. bilineata* closely resemble those of *Psettichthys* among other genera (Table 12). Both have alternating patches of pigment on dorsal and ventral body margins, although *Psettichthys* has a series of small patches on the dorsal and ventral finfold margins whereas *L. bilineata* has isolated patches along the finfolds. A series of postanal ventral melanophores is present in *L. bilineata* and absent in *Psettichthys*, in which postanal pigment is usually restricted to three or four large spots. Larvae of *L. bilineata* generally have much less pigment on the jaws and isthmus than do larvae of *Psettichthys*.

Size at stage of development varies among species (Table 13). Larvae of *L. bilineata* begin transformation at smaller lengths than larvae of *L. polyxystra* n. sp. or *L. mochigarei*. Larvae of *L. bilineata* also have a larger orbit, shorter snout-to-anus length, and a slenderer body (see Table 2).

The juvenile stages of most eastern North Pacific pleuronectids are poorly known. Traditional early life history descriptions typically describe developmental stages on the basis of eggs and larvae captured in plankton nets and usually do not include transitional larvae that undergo changes associated with a benthic existence. Plankton surveys routinely use nets that do not effectively sample bottom waters where many pleuronectid juveniles eventually settle.

Pleuronectid juveniles can be separated by several characters. Perhaps the most important character is the size at which transformation occurs, although data are scarce on when transformation is completed. Among taxa for which data are available, eastern North Pacific pleuronectids can be grouped into three categories based on approximate transformation sizes: <15 mm SL, 15–30 mm SL, and >30 mm SL. Genera with at least one species transforming at sizes <15 mm SL include *Limanda*, *Platichthys*, *Pleuronectes*, and *Pleuronichthys* (sensu Cooper and Chapleau, 1998). Genera with larvae that transform at much larger sizes (>30 mm SL) include *Atheresthes*, *Embassichthys*, *Glyptocephalus*, *Hippoglossoides*, *Microstomus*, and *Reinhardtius*. Larvae of *Lepidapsetta* generally undergo transformation between 15 and 25 mm SL. Other eastern North

Pacific pleuronectids that undergo transformation at similar sizes include *Acanthopsetta*, *Eopsetta*, *Hippoglossus*, *Isopsetta*, *Lyopsetta*, *Parophrys*, and *Psettichthys*.

Characters that separate juveniles further include meristics of vertebrae, median fin elements, and gill rakers (although gill rakers may not be fully formed); mouth size; and the shape of the lateral line. Generally juveniles of *Lepidopsetta* have lower meristics than juveniles of *Atheresethes*, *Eopsetta*, *Hippoglossoides*, and *Hippoglossus*. Juveniles of *Lepidopsetta* develop the highly arched lateral line during this stage (15–25 mm SL). A combination of mouth size, residual larval pigment on the blind side of early juveniles, lateral line shape, and, in larger juveniles, number of gill rakers may help to separate other similar-looking eastern North Pacific pleuronectids (*Acanthopsetta*, *Isopsetta*, *Lyopsetta*, *Parophrys*, and *Psettichthys*).

Identification of early life history stages of *Lepidopsetta* has been confused in the literature for many years. Hickman (1959) described egg and larval development of the sand sole, *Psettichthys melanostictus*, on the basis of material collected from Puget Sound, Washington. He illustrated six larvae identified as *Psettichthys* from specimens reared from eggs (his Figs. 1 and 2) and from larvae collected by net (his Figs. 3–6). His Figures 3 and 4 can be identified as *L. bilineata* from the alignment of dorsal and ventral midline melanophores on the postanal body.

In her extensive study of reproduction and development in North Pacific flatfishes, Pertseva-Ostroumova (1961) described the early life history stages of *L. bilineata* and *L. mochigarei*. The description of *L. bilineata* is based on material from collections off the Kuril Islands, off the eastern and western coasts of Kamchatka, and in the western Bering Sea. Larvae from these geographic areas are *L. polyxystra* n. sp.

Blackburn (1973) provided figures of two specimens of *L. bilineata* (his appendix Fig. C-2, A and B) in his survey of ichthyoplankton from Skagit Bay, Puget Sound. His discussion, however, is clearly based on the larvae of both eastern North Pacific species.

Garrison and Miller (1982) reviewed the reproductive characteristics of *L. bilineata*, but their sources either represent both species (Smith, 1936; Forrester, 1969; Forrester and Thompson, 1969) or *L. polyxystra* n. sp. alone (Shubnikov and Lisovenko, 1964; Shvetsov, 1979). Ahlstrom et al. (1984) correctly illustrated *Psettichthys* larvae but presented data and a figure for *L. bilineata* (their Fig. 351b) based on Figure 22 (4) of Pertseva-Ostroumova (1961), now identified as *L. polyxystra* n. sp. Okiyama (1988) also presented material for *L. bilineata*, based on Figure 23(1) of Pertseva-Ostroumova (1961), which therefore represents *L. polyxystra* n. sp.

Matarese et al. (1989) separated larvae of *Lepidopsetta* from *Psettichthys*. Their description and figures of *L. bilineata* are based on what we now refer to as *L. polyxystra* n. sp., whereas the descriptions and figures of "*Lepidopsetta* 2" are now referred to as *L. bilineata*. Charter and Moser (1996) presented figures of both *Psettichthys melanostictus* and *L. bilineata* but, because Pertseva-Ostroumova (1961) was cited as a source for *L. bilineata*, some descriptive data are suspect. Data for *L. bilineata*, particularly in the

introductory tables, may be based in part on *L. polyxystra* n. sp. (see tables "Pleuronectidae," pages 1370–1373, Charter and Moser, 1996).

Key to juveniles and adults >30 mm of species of *Lepidopsetta*

- 1a Preopercular pores 8–13; lateral-line pores 95–119; sum of scales above and below lateral line 91–103; supraorbital pores 1–3; total gill rakers on first arches ≤10, on upper part of first arch ≤3 . . . *L. mochigarei*
southern Sea of Okhotsk to Korea
- 1b Preopercular pores 5–7; lateral-line pores 70–91; sum of scales above and below lateral line 65–88; supraorbital pores 1–8; total gill rakers on first arch 6–14 . . . 2
- 2a Total gill rakers on first arch typically ≥10, on upper part of first arch ≥3; supraorbital pores 1–2, rarely 3–7; blind side creamy white . . . *L. polyxystra* n. sp.
Puget Sound to Sea of Okhotsk
- 2b Total gill rakers on first arch typically ≤10, on upper part of first arch ≤3; supraorbital pores 3–8; blind side with extensive bright white highlights . . . *L. bilineata*
Baja California to southeastern Bering Sea

Lepidopsetta bilineata (Ayres, 1855a)

Southern rock sole

Figs. 1–6, 10, 12, 14–18; Tables 2–11, 13–14

Platessa bilineata Ayres, 1855a:2 (original description, one specimen, apparently lost, sex and size unknown, fish markets of San Francisco Bay, California).

Platichthys umbrosus Girard, 1856:136 (original description, one specimen, apparently lost, sex unknown, ca. 190 mm TL, Cape Flattery, Washington).

Pleuronectes perarcuatus Cope, 1873:32 (original description, one specimen; holotype, ANSP 8725, sex undetermined, 108 mm SL, Gulf of Alaska, "Sitka" or "Unalaska").

Lepidopsetta bilineata umbrosa (in part) Jordan and Evermann, 1898:2643 (new combination, "Puget Sound and northward").

Lepidopsetta bilineata bilineata Taranets, 1937:144 (new combination, keys).

Pleuronectes bilineata Sakamoto, 1984a:99 (new combination, phylogenetics).

Neotype

CAS 42650, 1(207.6 mm), Calif., Gulf of the Farallones, Sta. F43(2)N, M. Moriguchi, August–September 1978.

Other material examined

A total of 380 adult and juvenile specimens, 22.7–426 mm, including the neotype listed above, was examined. Sixty-four larvae were examined.

Adults Bering Sea: UW 041696, 3(222–245 mm), N of Unimak I., 55.0213°N, 164.6009°W. Aleutian Islands: SIO 94-164, 1(167 mm) of 10(103–193 mm), Unimak Pass, 54°15.1'N, 165°57.6'W, 4 June 1994; UW 041695, 3(170–210), Aleutian Is., NE of Umnak I., 53.44°N, 168.4944°W; Gulf of Alaska: ABL uncat, 1(153 mm), Ursus Channel, San Fernando I., 1 November 1956; ABL 64-696, 1(138 mm), Gore Point, S of Kenai Peninsula, 28 July 1963; ABL 67-211, 4(197–234 mm), Auke Bay, 19.2 km NW of Juneau, 22 May 1962; ABL 71-5, 2(200.5–205.5 mm), Baranof I., Point Conclusion, 17 May 1971; OS 6447, 3(166.1–184.6 mm), 57°10'N, 151°40.5'W, 77 m, 20 September 1978; OS 2156, 1(75.0 mm), Revillagigedo I., Ward Cove, 26 July 1949; OS 2175, 1(102.4 mm), Revillagigedo I., Ward Cove, 26 August 1949; SIO 72-219, 1(251 mm), Lituya Bay, 9.3 km SW of Harbor Pt., 25 June 1961; SIO 72-258, 1(289 mm), Baranof I., Katlian Bay, 57°10'N, 135°20'W; SIO 72-225, 1(288 mm), 2°E of Kodiak I., 6 May 1962; SIO 76-300, 1(187.5 mm) of 28(145–280 mm), Kodiak shelf, 57°40'N, 150°37'W, 23 June 1976; SIO 69-478, 3(112–170 mm) of 7(51–195 mm), Afognak I., Kitoi Bay, NE of Kodiak I., 16–21 April 1968; UW 040267, 1(330 mm), off Kodiak; UW 044021, 1(255 mm), 55.8088°N, 158.7503°W, 67 m, 10 June 1996; USNM 054286, 1(358 mm), Ketchikan, Sta. TT2120, RV *Albatross*; USNM 130739, 1(252 mm), Prince William Sound, Macleod Harbor, 16 March 1941; UW 01666, 1(132 mm), Alexander Archipelago, off Wrangell I., 1 December 1931; UW 008376, 1(240 mm), Ketchikan, 23 September 1949; UW 040902, 1(182 mm), Prince William Sound, 1989; UW 008292, 1(162 mm), Southeast Alaska, 26–31 March 1950; UW 018837, 2(222.5–230.5 mm), 11.7 km NNW of Triangle I., 50°58.1'N, 129°4.9'W, 19 August 1960; UW 40264, 1(342 mm), 54.039°N, 165.8153°W; UW 27679, 23(20.5–57.4 mm), Prince William Sound; UW 044010, 1(240 mm), 59.4918°N, 151.6185°W, 41 m, 27 February 1996; UW 044028, 1(292 mm), 59.4885°N, 151.6062°W, 30 m, 27 February 1996; UW 044025, 2(210–285 mm), Kachemak Bay, 12 May 1996; UW 040268, 1(290 mm), Kodiak I.; UBC 65-525, 1(290 mm), off Baranof I.; UW 044013, 7(287–426 mm), 56.5°N, 153.5°W, R. Bonaduh; UW 041801, 6(270–335 mm), 54°N, 160.74°W, British Columbia; UW 083483, 33.5 mm, off Vancouver Island, 48°39.5'N, 125°55.2'W, 19 September 1977. SIO 63-202, 1(247 mm), Strait of Georgia, Fraser R.; USNM 31993, 1(158.5 mm), Carter Bay, June 1882; UBC 53-85, 1(172 mm), Vancouver I.; UBC 53-50, 1(57.3 mm), Vancouver I.; UBC 53-68, 1(105 mm), Vancouver I.; UBC 53-50, 1(57.3 mm), Vancouver I., Departure Bay, 49.2167°N, 123.95°W; UBC 53-301, 7(101.5–177 mm), Vancouver I., Baynes Sound; UBC 53-245, 1(144.8 mm), Vancouver I., Burrard Inlet; UBC 55-281, 1(32.9 mm), Vancouver I., Departure Bay, 49.2167°N, 123.95°W; UBC 56-8, 1(220.5 mm); UBC 55-496, 3(217–235 mm), Point Gray, 3.2 km SE of North Arm of Fraser R.; UBC 56-519, 5(205–233 mm), Vancouver fish docks; UBC 61-393, 3(59–88 mm), Bute Inlet; UBC 61-484, 2(145–167 mm), Vancouver I., Burrard Inlet, 25 October 1961; UBC 61-609, 9(38.5–123 mm), Bute Inlet; UBC 61-232, 2(245 mm and one head only), Hecate Strait; UBC 60-416, 1(205 mm), Queen Charlotte Is., Gillat Arm; UBC 63-910, 1(148 mm), Howe Sound; UBC 63-732, 10(68–140 mm), off Keats I.; UW 044026, 1(306.5 mm),

48.57723°N, 124.7803°W, 25 August 1995; UW 044027, 2(293–308 mm), 48.74507°N, 125.9744°W, 28 August 1995; UBC 65-676, 6(44–142 mm), Graham I., McIntyre Bay; UBC 62-93, 6(80–142 mm), Nass Bay; UBC 61-686, 1(62.8 mm), S of Vargas I., 5 July 1934; UBC 61-621, 1(50.5 mm), Snake I., near Nanaimo, 8 May 1933; UBC 61-610, 2(139–142 mm), Work Channel, head of Trail Bay, 16 July 1951; UBC 61-674, 1(60 mm), Dean Channel, off Nescall Bay; UBC 62-94, 1(94 mm), Sydney Inlet; UBC 81-3, 1(201 mm), Vancouver I., Grappler Inlet; UBC 76-7, 1(135 mm), English Bay, 20 January 1962. Washington, Oregon, and California: USNM 054392, 1(292 mm), near Port Townsend, TT2838, RV *Albatross*; USNM 27299, 2(150–246 mm), Puget Sound, 1880; UW 041090, 2(196.0–196.5 mm), Agate Pass, 3 April 1950; UW 041089, 1(229 mm), Agate Pass, 3 April 1950; UW 6070, 7(61–133 mm), San Juan Islands, East Sound, 3 March 1937; UW 06134, 2(53–63.5 mm), N of Maury I., 4 December 1948; UW 014838, 2(65–68 mm), Golden Gardens Beach, 14–15 May 1952; UW 014380, 2(101–108 mm), near Hat I., 29 May 1936; UW 044011, 1(145 mm), San Juan Islands, East Sound, 18 February 1964; UW 017115, 1(178 mm), Port Orchard Channel, 2 February 1964; UW 015423, 1(169 mm), Shilshole Bay; UW 000782, 2(147–156.5 mm), Alki Point, 8 March 1930; UW 005522, 11(46.6–159.5 mm), Edmonds, 18 August 1947; UW 018663, 1(60.5 mm), San Juan Islands, East Sound, 11 December 1964; UW 040665, 2(54–58 mm), Port Townsend Bay, 5 January 1979; UW 040686, 6(114.3–167.3 mm), West Point, 3 October 1978; UW 025723, 4(52.1–230.5 mm), Port Townsend Bay, 5 December 1978–5 January 1979; UW 025721, 3(166–208 mm), Golden Gardens, 22 July 1981; UW 006109, 1(154.5 mm), Alki Point, 3 March 1939; UW 017840, 1(211 mm), S end of Port Susan, 6 May 1950; UW 025719, 12(103.2–164.5 mm), Murden Cove, 22 April 1980; UW 025727, 2(116.5–169.5 mm), West Point, 29 March 1979; UW 005135, 8(22.7–70.6 mm), Alki Point, 5 April 1938; UW 025197, 1(77.3 mm; cleared-and-stained), Meadow Point; UW 044006, 11(135–250.5 mm), Nisqually, 47.1578°N, 122.6693°W, 16 May 1996; UW 040269, 10(209–259 mm), Puget Sound, 47°19.48'N, 122°33.8'W, 10 May 1996; UW 029670, 49(125.3–283.5 mm), Colvos Passage off Vashon I., 47.5°N, 122.4167°W, 18 July 1949; UW 025726, 5(125–175 mm), Puget Sound, West Point, 3 October 1978; UW 025720, 7(130–185 mm), Puget Sound, West Point, 3 April 1979; UW 041319, 6(122–202 mm), Puget Sound, West Point; UW 041330, 1(225 mm), Puget Sound, Portage Bay; UW 041301, 1(245 mm), Puget Sound, Port Townsend Bay; OS 15509, 4(226.5–287.4 mm), Cobb Seamount, 46°50'N, 130°50'W, 20 August 1992; OS 13792, 1(180.3 mm), 44°54.2667°N, 124°10.0667°W; OS 13500, 1(417 mm), Cobb Seamount, 46°50'N, 130°50'W; OS 13499, 1(330 mm), 44°52.2667°N, 124°09.55'W; OS 7482, 1(223.3 mm), off Newport; OS 14732, 1(132.2 mm), 44°40.7'N, 124°09'W; OS 14690, 1(189.4 mm), 44°37'N, 124°11.1'W; OS 6208, 4(137.3–222.8 mm), off Newport, 30 September 1978; OS 7477, 1(173.7 mm), 44°37.4'N, 124°08.9'W; CAS 18553, 1(198.5 mm), Calif., San Francisco Bay, 14 May 1931; CAS 31832, 1(205 mm), Calif., Gulf of the Farallones, 37°44'N, 122°40'W, October 1973; CAS 40341, 1(347.4 mm), Calif., 22.6 km NW of Pt. Pinos, 34°47.5'N, 122°7.8167°W; CAS-SU 111615, 1(335.0 mm),

San Francisco Market, May 1895; CAS 49152, 1(229.5 mm), Calif., Sonoma, Bodega Bay, 18 October 1981; SIO 88-119, 1(277 mm), Calif., south of La Jolla; SIO H48-22, 1(261 mm), Calif., south of La Jolla; SIO 63-241, 1(243 mm), Tanner Bank, Calif., 32°42.5'N, 119°6.5'W, 17 May 1963; SIO 65-460, 1(284 mm), Calif., ridge between Tanner and Cortez Banks, 26 September 1965; SIO 65-6-64A, 1(210 mm), Calif., Tanner Bank, 32°42'N, 119°08'W, 15 January 1965; SIO 63-732-64A, 1(183 mm), Calif., Catalina I., off Avalon, 22 March 1962; SIO 85-145, 2(74–86 mm), Calif., Navarro Head, 39°05.7'N, 123°E44.95'W, 60.4–110.5 m, 17 August 1985; LACM W54-382, 7(178.5–247 mm), 1.6 km W of Santa Barbara I., 33°08.15'N, 119°04.1333'W, 31 October 1954; LACM W66-67, 1(198.5 mm), off San Simeon Point, 13 November 1966; LACM W54-380, 2(274–275 mm), 1.6 km E of Santa Barbara I., 30 October 1954; LACM 44390-1, 1(282 mm), off Palos Verdes, 22 February 1988; LACM 31966-8, 8(176.5–357 mm), Humboldt Co., 8 km S of Shelter Cove, 7 August 1971; LACM 241, 4(153–320 mm), Calif., San Francisco; OS 972, 1(201.2 mm), southern Calif.; LACM 35690-3, 2(83–164.5 mm), Calif., S end of Tanner Bank; UW 044009, 9(143–252.5 mm), 37.781°N, 122.9288°W, 26 June 1995; UW 040262, 1(250 mm), 48.74317°N, 125.7785°W, 27 September 1992; UW 041698, 1(223 mm), 35.0935°N, 120.7774°W, 15 June 1995; UW 041803, 1(358 mm), 47.0839°N, 124.748°W, 8 August 1995; UW 041802, 1(376 mm), 46.91147°N, 124.7292°W, 3 August 1995; UW 041903, 2(290–347 mm), 46.91308°N, 124.4756°W, 5 August 1995; Mexico: CAS 2484, 1(226.3 mm), Baja California, off Cortez Banks, 21 August 1932.

Larvae 64 specimens (2.7–19.0 mm) examined: Western Gulf of Alaska: UW 083400, 2(10.8–12.3 mm), 54°10.8'N, 165°24.3'W, 0–55 m depth, Methot net, 30 July 1991; UW 083401, 1(10.9 mm), 54°38.5'N, 160°51.2'W, 0–98 m depth, Methot net, 30 July 1991; UW 083402, 1(12.0 mm), 56°11.6'N, 157°21.7'W, 0–129 m depth, Methot net, 27 July 1991; UW 083403, 1(14.0 mm), 54°36.2'N, 162°16.2'W, 0–87 m depth, Methot net, 30 July 1991; UW 083404, 1(14.1 mm), 55°43.8'N, 157°34.6'W, 0–105 m depth, Methot net, 27 July 1991; UW 083405, 2(14.4–15.6 mm), 55°43.0'N, 159°49.4'W, 0–108 m depth, Methot net, 25 July 1991; UW 083406, 1(15.5 mm), 53°59.8'N, 165°51.0'W, 0–50 m depth, Methot net, 31 July 1991; UW 083407, 2(15.9–16.0 mm), 55°18.0'N, 160°11.4'W, 0–115 m depth, Methot net, 24 July 1991; UW 083408, 1(16.0 mm), 55°17.7'N, 160°11.7'W, 0–115 m depth, Methot net, 24 July 1991; UW 083445, 1(13.3 mm), 56°11.6'N, 158°03.6'W, 0–141 m depth, Methot net, 25 July 1991; UW 072255, 5 of 6(2.7–8.6 mm), 57°01.1'N, 156°19.2'W, 0–95 m depth, bongo net, 3 June 1990; UW 072453, 2 of 4(6.2–6.5 mm), 57°17.2'N, 155°27.6'W, 0–102 m depth, bongo net, 5 June 1990; UW 072126, 2(6.6–7.3 mm), 56°54.0'N, 156°29.5'W, 0–84 m depth, bongo net, 3 June 1990; UW 071455, 1(6.7 mm), 57°60.0'N, 153°59.3'W, 0–103 m depth, bongo net, 28 May 1990; UW 072087, 1(8.1 mm), 56°39.8'N, 156°20.0'W, 0–102 m depth, bongo net, 3 June 1990; UW 072264, 1(8.7 mm), 57°09.1'N, 156°09.1'W, 0–100 m depth, bongo net, 3 June 1990; Gulf of Alaska: UW 083484, 1(19.0 mm), 59°37.8'N, 151°44.2'W, 34 m depth, 17 July 1996; UW 083409, 1(16.4 mm), 58°19.5'N, 150°53.0'W,

64 m depth, bongo net, 22 July 1977; UW 083410, 1(6.3 mm), 57°61.1'N, 151°17.4'W, 0–35 m depth, Tucker net, 26 June 1978; UW 083411, 1(9.7 mm), 56°42.3'N, 153°33.4'W, 28–70 m depth, Tucker net, 28 June 1978; UW 083412, 1(11.0 mm), 57°00.8'N, 153°28.3'W, 0 m depth, neuston net, 14 September 1978; UW 083413, 2(5.1–6.2 mm), 57°10.7'N, 156°01.3'W, 0–100 m depth, Tucker net, 4 June 1988; UW 083414, 1(6.6 mm), 56°21.0'N, 157°03.8'W, 0–100 m depth, Tucker net, 6 June 1988; UW 083415, 1(6.4 mm), 56°47.3'N, 155°26.0'W, 0–105 m depth, Tucker net, 23 May 1988; UW 083416, 1(6.5 mm), 57°03.8'N, 156°01.8'W, 0–101 m depth, Tucker net, 4 June 1988; UW 083417, 1(6.6 mm), 56°47.3'N, 155°25.9'W, 0–101 m depth, Tucker net, 4 June 1988; UW 083418, 1(7.1 mm), 57°10.8'N, 156°29.9'W, 0–102 m depth, Tucker net, 4 June 1988; UW 083419, 1(8.3 mm), 56°38.9'N, 156°31.5'W, 0–101 m depth, Tucker net, 2 June 1988; UW 083420, 1(10.2 mm), 56°46.7'N, 156°18.3'W, 0–91 m depth, Tucker net, 2 June 1988; UW 083421, 1(10.6 mm), 57°15.0'N, 155°53.6'W, 0–101 m depth, Tucker net, 4 June 1988; UW 083422, 3(3.3–3.4 mm), 57°55.6'N, 151°02.3'W, 0–76 m depth, bongo net, 13 May 1991; UW 083423, 1(3.9 mm), 5°43.8'N, 154°02.1'W, 0–100 m depth, bongo net, 24 May 1991; UW 083424, 1(4.7 mm), 55°53.9'N, 155°59.8'W, 0–75 m depth, bongo net, 23 May 1991; UW 083425, 1(4.9 mm), 57°36.9'N, 155°28.3'W, 0–101 m depth, bongo net, 24 May 1991; UW 083426, 1(3.6 mm), 56°40.7'N, 155°10.7'W, 0–61 m depth, bongo net, 8 May 1992; UW 083427, 1(6.0 mm), 56°58.4'N, 156°06.2'W, 0–100 m depth, bongo net, 14 May 1992; UW 083428, 2(3.5–4.3 mm), 55°27.2'N, 157°39.3'W, 0–88 m depth, bongo net, 19 May 1992; UW 083429, 1(3.8 mm), 55°17.0'N, 157°44.8'W, 0–72 m depth, bongo net, 19 May 1992; UW 083430, 1(4.6 mm), 55°22.5'N, 156°56.8'W, 0–80 m depth, bongo net, 19 May 1992; UW 083431, 1(7.9 mm), 55°16.0'N, 156°15.0'W, 0–102 m depth, bongo net, 18 May 1992; UW 083432, 1(7.3 mm), 55°55.3'N, 156°15.3'W, 0–216 m depth, bongo net, 21 May 1992; UW 083443, 1(3.2 mm), 57°01.1'N, 156°19.2'N, 0–95 m depth, bongo net, 3 June 1990; Puget Sound: UW 083433, 1(9.6 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 9 May 1994; UW 083434, 1(9.7 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 5 May 1989; UW 083435, 1(11.2 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 27 March 1991; UW 083436, 1(11.4 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 16 July 1987; UW 083437, 1(13.3 mm), 48°1.0'N, 123°0.0'W, reared, 4 May 1989; UW 083438, 1(13.4 mm), 48°1.0'N, 123°0.0'W, reared, 4 May 1989; UW 083439, 1(14.4 mm), 48°1.0'N, 123°0.0'W, 0 m depth, dip net (26 April 1989), reared (20 May 1989); UW 083440, 1(15.2 mm), 48°1.0'N, 123°0.0'W, 0 m depth, dip net (26 April 1989), reared (20 May 1989); UW 083441, 1(15.6 mm), 48°1.0'N, 123°0.0'W, 0 m depth, dip net, 1 July 1989; UW 083442, 1(11.4 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 16 July 1987; UW 083444, 1(9.3 mm), 47°34.15'N, 122°32.3'W, 0 m depth, dip net, 1 June 1989.

Diagnosis

This species of *Lepidopsetta* has the following combination of characters in adults: total gill rakers on first arch 6–11; on upper arch 1–3, rarely 4, with at least one rudi-

mentary; total gill rakers on second arch 6–11; supraorbital pores 3–9; preopercular pores 5–7; lateral-line pores 70–91; sum of scales above and below lateral line 65–88; interorbital narrow; blind-side coloration white, with glossy highlights along myotome margins increasing anteriorly.

Larvae are distinguished from other species of *Lepidopsetta* by the following characters: body deep, snout-to-anus length short; hatching, flexion, and transformation at comparatively smaller sizes; preflexion pigment pattern with pigment patches along distal edges of dorsal and anal finfolds, four prominent spots along dorsal midline (in a pattern resembling alternating dorsal and ventral spots, with posteriormost dorsal spot coalescing with a corresponding ventral patch to form a bar), and a series of small ventral midline melanophores extending from gut to last myomere; flexion pigment pattern with distinctive anterior dorsal midline spot and posteriormost dorsal spot forming a bar with corresponding ventral patch; pectoral-fin rays unpigmented.

Description of adults (Fig. 15)

Body ovate, greatest depth 40.8–57.0 (47.0)% SL, scales above lateral line 25–43 and scales below lateral line 27–53; head relatively acute, length 24.0–32.9 (28.2)% SL; dorsal margin of head at dorsal-fin origin concave, snout length 3.1–6.1 (4.5)% SL (12.4–22.4 (16.1)% HL); ocular-side maxilla length 25.3–32.5 (27.9)% HL; blind-side maxilla relatively long, length 25.2–41.2 (31.3)% HL; ocular-side mandible length 38.3–46.1 (41.9)% HL; teeth 5–10 on ocular-side premaxilla, 20–27 on blind-side premaxilla and 10–12 on ocular-side dentary, 23–29 on blind-side dentary; gill rakers of first arch typically broad and robust, 6–11 total, 1–4 on upper arch, 5–7 on lower; gill rakers of second arch 6–11 total, 1 on upper and 5–10 on lower arch; dorsal orbit larger than eye length, orbit length 23.4–32.5 (28.1)% HL, dorsal eye length 17.9–30.3 (24.2)% HL; ventral eye length 18.2–35.4 (24.8)% HL; interorbital narrow, up to 3 scales at narrowest portion, 2.1–6.0 (3.5)% HL; cheek with 9–16 scales, length 28.1–41.8 (34.2)% HL, depth 13.9–24.2 (19.2)% HL; preopercular pores 5–7; ocular-side suborbital pores 14–29; blind-side suborbital pores 6–13; lateral-line pores 70–91, lateral-line arch length 49.3–58.1 (54.3)% HL, its depth 24.8–37.1 (30.2)% of its length; both anterior and posterior supratemporal branches relatively long, anterior pores 2–12, posterior pores 8–30; supraorbital canal long, extending to dorsal rim of dorsal orbit near insertions of dorsal-fin rays 3–4, pores 3–9; ocular-side pectoral-fin length 12.2–18.2 (15.2)% SL (43.6–66.2 (53.9)% HL); blind-side pectoral-fin length 6.7–12.2 (9.9)% SL (23.2–44.3 (35.0)% HL), about equal to ocular-side pelvic-fin length 7.6–12.5 (9.8)% SL

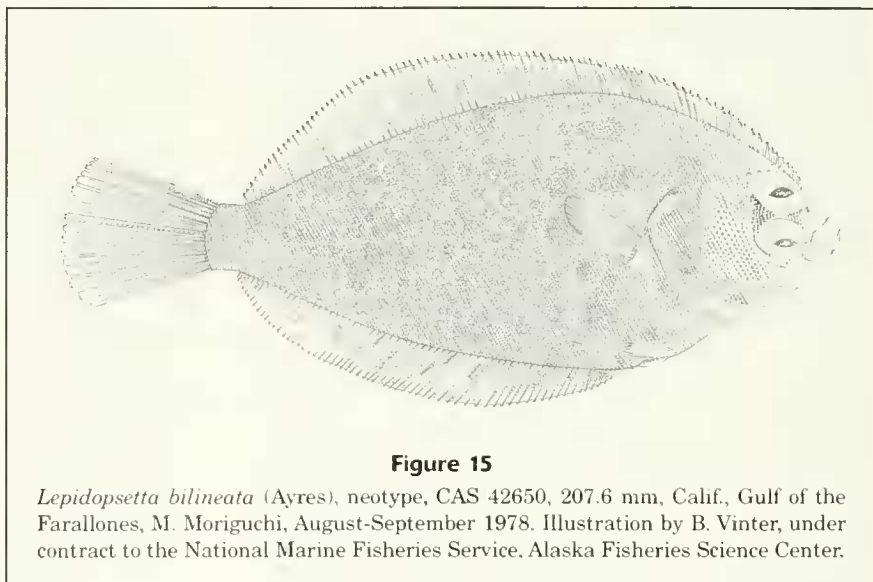


Figure 15

Lepidopsetta bilineata (Ayres), neotype, CAS 42650, 207.6 mm, Calif., Gulf of the Farallones, M. Moriguchi, August–September 1978. Illustration by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

(26.7–44.7 (34.8)% HL); dorsal fin with 67–89 rays, height 10.7–16.5 (13.3)% SL, in specimens with 72–79 rays supported by 71–78 pterygiophores, 9–11 anterior to first neural spine; anal fin with 54–77 rays, in specimens with 54–62 rays supported by 53–60 pterygiophores; caudal peduncle relatively slender, least depth 8.2–12.3 (10.2)% SL (29.6–43.0 (36.2)% HL; 90.0–152.4 (112.6)% caudal peduncle length); greatest depth 10.5–14.3 (12.1)% SL (37.2–53.0 (42.8)% HL); caudal peduncle length 7.2–10.9 (9.1)% SL (25.5–42.2 (32.4)% HL); caudal-fin length 15.3–23.6 (20.8)% SL. Vertebrae 40–41, with 11 precaudal and 29–30 caudal.

Scales around head and those scattered posteriorly on ocular side moderately rough with columnar tubercles in large adults; strong spines in small adults and juveniles. Urogenital flap darkly pigmented in 21–58 mm juveniles.

In life, blind side in adults translucent to bright white, with glossy highlights along edges of myotomes; in juveniles, primarily translucent, and having reduced glossy areas especially prominent over the head. When preserved, blind side of all individuals uniform creamy white to yellow-brown. Ocular side slightly more green than that of congeneric in Puget Sound.

Remaining description as for genus. Largest specimen examined 426 mm (UW 044012). Maximum size reported ca. 540 mm (580 mm TL⁶).

Description of juveniles (Fig. 16)

Most individuals were collected on bottom (Fig. 16A) by 19.0 mm; newly settled juveniles with dorsal eye completely migrated; median fin rays formed; lateral line nearly formed; expanded anteriormost anal-fin pterygiophore well devel-

⁶ Resource Assessment and Conservation Engineering (RACE) Division, 1996. Unpubl. data from RACE database, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

oped. Preanal pigment increased along head and gut; postanal pigment smaller and distributed in random patches; urogenital papilla darkly pigmented throughout its length. Blind side with pigment similar to that of postflexion larvae. Orbit length larger, mouth smaller, body depth less, gill-raker counts on lower arch less, and distance from pelvic-fin origin to anal-fin origin greater than in *L. polyxystra* n. sp. Pelvic- and pectoral-fin rays formed.

By 30.0 mm, pigmentation has increased along body, with darker patches and spots throughout (Fig. 16B) obscuring pigmented urogenital papillae. Lateral line more fully developed; supraorbital canal pores visible.

Description of larvae (Fig. 17)

Snout-to-anus length is 32.9–34.6% SL, remaining constant during development; body depth 4.7–35.7% SL, increasing with development, sharply after flexion; head length 13.3–29.3% SL, increasing with development, sharply after flexion; snout length 22.6–20.7% HL, remaining constant during development; orbit length 51.9–23.8% HL, decreasing with development (Table 2). Total myomeres 37–44.

Larvae hatching at small lengths, at sizes less than 3.0 mm, yolk absorbed by 2.7–4.5 mm. Preflexion larvae ranging in size from 3.8 to 6.6 mm; flexion larvae, from 6.4 to 11.1 mm; postflexion larvae from 10.8 to 16.0 mm. Transformation occurring at lengths as small as 10.0 mm (often accompanied by a decrease in total body length); postsettlement juvenile stage usually attained by 20.0 mm (Table 13).

Preanal pigment present initially along lower jaw and ventral side of cleithral region, increasing with development to snout, upper jaw, and isthmus. Pigment ventrally along gut and dorsally on anus; by flexion a distinct patch of melanophores along the posterior edge of the gut; pigment increases laterally with development.

Postanal pigment present as melanophores along distal edges of dorsal and anal finfolds; four distinct pigment areas along the dorsal midline, anterior (first) spot begins 1–5 myomeres after anus at about myomere 12–16, second spot begins at about myomere 23–26, third spot begins at about myomere 33–46, and the fourth spot begins at about myomere 41–42 (after initially forming as a dorsal midline

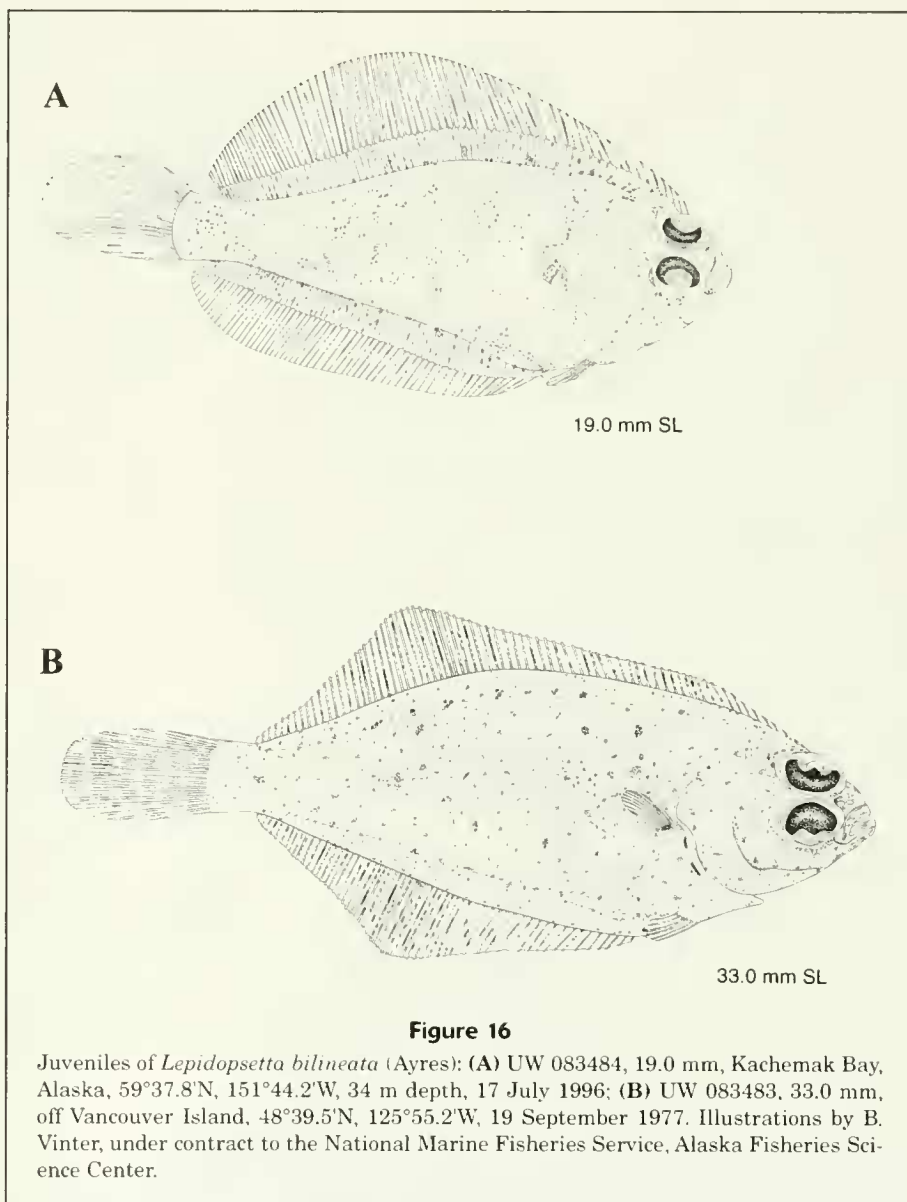


Figure 16

Juveniles of *Lepidopsetta bilineata* (Ayes): (A) UW 083484, 19.0 mm, Kachemak Bay, Alaska, 59°37.8'N, 151°44.2'W, 34 m depth, 17 July 1996; (B) UW 083483, 33.0 mm, off Vancouver Island, 48°39.5'N, 125°55.2'W, 19 September 1977. Illustrations by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

patch, the posteriormost spot coalesces with ventral patch to form a caudal bar); series of melanophores from the gut along the ventral midline beginning in a double row, changing to a single row posterior to the ventral stripe of the caudal bar; several additional melanophores along the ventral midline posterior to the caudal bar, pigment above and below the tip of the notochord. By transformation, the third dorsal midline patch and opposing ventral patch expand to form an indistinct bar; other patches of pigment form in myosepta and continue into the dorsal and anal pterygiophores and fin rays.

Distribution (Figs. 6, 10, 12, 18)

Lepidopsetta bilineata ranges from the continental shelf north and south of the Islands of Four Mountains in the eastern Aleutian Islands and in the southern Bering Sea

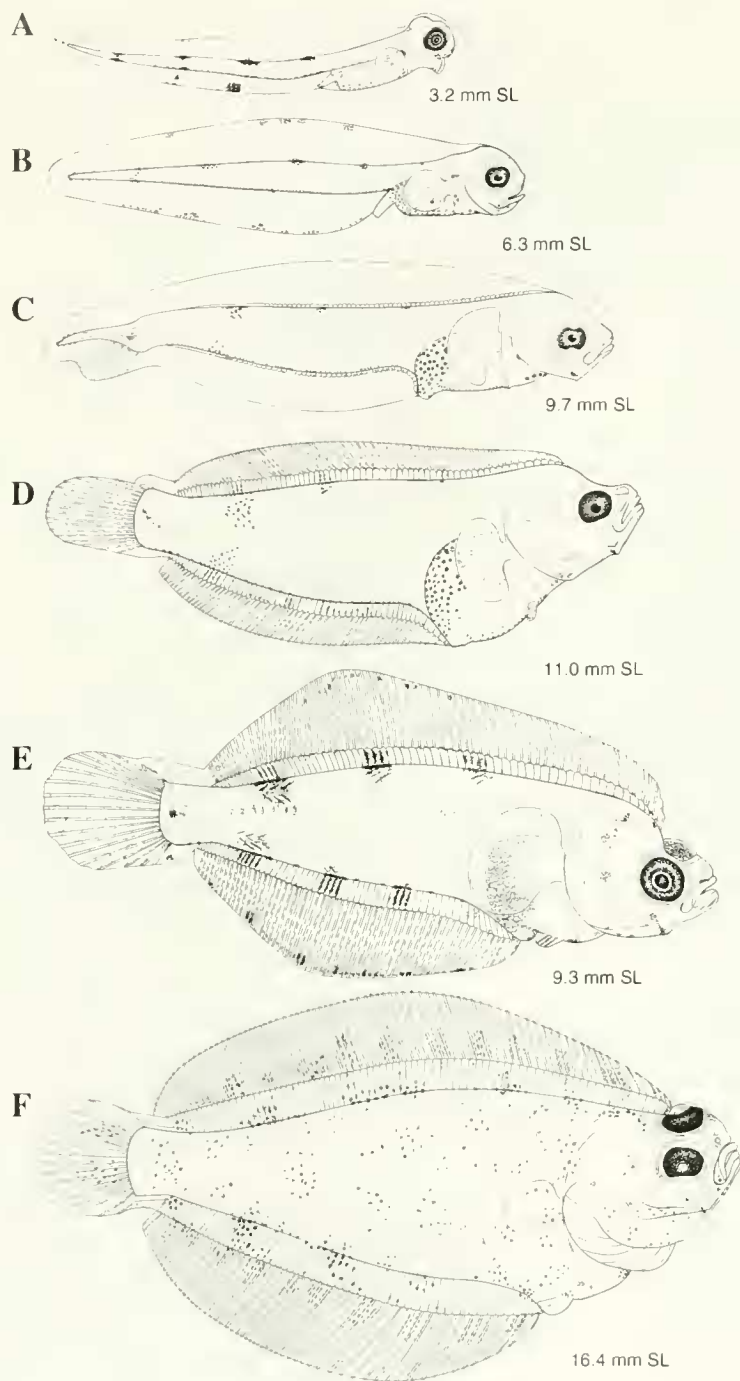


Figure 17

Larvae of *Lepidopsetta bilineata* (Ayres): (A) UW 083443, 3.2 mm, Gulf of Alaska, AFSC, 3 June 1990 ; (B) UW 083410, 6.3 mm, Gulf of Alaska, AFSC, 26 June 1978 (Matarese et al., 1989); (C) UW 083411, 9.7 mm, Gulf of Alaska (Matarese et al., 1989), AFSC, 28 June 1978; (D) UW 083412, 11.0 mm, Gulf of Alaska, AFSC, 14 Sept 1978; (E) UW 083444, 9.3 mm, Puget Sound, AFSC, 1 June 1989; (F) UW 083409, 16.4 mm, Gulf of Alaska, AFSC, 22 July 1977 (Matarese et al., 1989). Illustrations by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

on the Slime Bank north of Unimak I., to Cortez Banks, Baja California, Mexico. It is common from the northern Gulf of Alaska to Puget Sound and is locally abundant along the coasts of Washington, Oregon, and California. Larvae have been collected from just south of the Aleutian Islands to Tanner Bank, Mexico (Moser et al., 1993; Charter and Moser, 1996).

Habitat

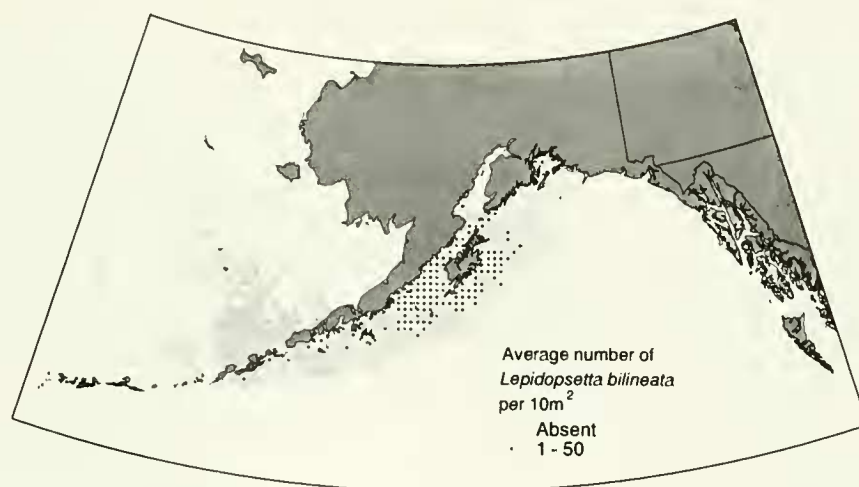
Adults were collected over sand and gravel substrates to depths of 339 m (RACE⁶). Larvae were collected over depths <1000 m.

During our 22-year sampling period, larvae were less common than those of *L. polyxystra* n. sp. in spring ichthyoplankton surveys conducted in the Gulf of Alaska. Larvae appeared in larger numbers later in the season (June) and the highest densities occurred from Kodiak Island to the eastern Gulf of Alaska (Table 14; Fig. 18). In the CalCOFI region, larvae were collected from February to July; peak abundance was in May (Charter and Moser, 1996). Larvae were collected more frequently and in higher densities closer to the coastline (within 55.6 km, Moser et al., 1993).

Life history

In *L. bilineata* taken off the coast of Oregon, brittlestars of the genus *Ophiuro* dominated the diet, and polychaetes and mollusks constituted much of the remainder (Kravitz et al. 1976). Adults from the Gulf of Alaska and Aleutian Islands are often infested with the parasitic copepods *Nectobranchia indivisa* and *Naobranchia occidentalis*.⁷ Both parasites were previously recorded in *Lepidopsetta* by Kabata (1988). For both parasite species, *L. bilineata* was significantly less infested than *L. polyxystra* n. sp.⁶ The maximum recorded age for female *Lepidopsetta* is 18 yr at 49 cm FL and for a male is 17 yr at 40 cm FL (Levings, 1967; Forrester, 1969). For early life history information, see generic account.

⁷ Zimmermann, M. and R. Harrison. 1998. Personal commun. Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

**Figure 18**

Distribution and density (average number per 10 m²) of *Lepidopsetta bilineata* in the Gulf of Alaska and Bering Sea, 1972–1994.

Table 14

Monthly collections of larvae of *Lepidopsetta* in the Gulf of Alaska and Bering Sea (1972–1994). Mean density (number per 10 m²) followed below by the standard deviation of the mean in parentheses.

Taxon	Month												Overall
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>L. bilineata</i>	0 (0)	0 (0)	0 (0)	0.0139 (0.0059)	0.568 (0.0592)	1.73 (0.243)	0.15 (0.0553)	0 (0)	0.116 (0.0872)	0.0311 (0.0311)	0 (0)	0 (0)	0.414 (0.0357)
<i>L. polyxystra</i> n. sp.	0 (0)	0 (0)	0.456 (0.204)	5.80 (0.633)	7.06 (0.383)	4.44 (0.481)	0.659 (0.018)	0 (0)	0.09 (0.0634)	0.0386 (0.0386)	0 (0)	0 (0)	5.34 (0.289)
Total observations	115	163	704	2926	2678	861	333	0	144	138	585	11	7502

Etymology

The specific name is derived from the Latin *bilineata*, meaning “two lined”, a reference to the bifurcate supratemporal branch of the lateral line.

Comments

Basing his work on an account first published in *The Pacific* (Ayres, 1855a) and subsequently reprinted in the *Proceedings of the California Academy of Sciences* (Ayres, 1855b), Ayres described his specimen of *Platessa bilineata* at the California Academy of Natural Sciences (CAS) in 1855. The specimen has not been located at CAS⁸ (where it may have been destroyed in the 1906 San Francisco earth-

quake and subsequent fire, Springer and Anderson, 1998), ANSP,⁹ LACM,¹⁰ or USNM.¹¹ Because *L. bilineata* may be easily confused with *L. polyxystra* n. sp., especially in the Gulf of Alaska and Puget Sound, we therefore designated CAS 42650, collected in the Gulf of Farallones off California, as the neotype of *L. bilineata*. Ayres obtained his specimen from the San Francisco fish market and noted that, although not common, the species was taken in San Francisco Bay. Lockington (1879a) noted that *L. bilineata* was most commonly caught “at or near the Farallone Islands” for the San Francisco markets.

⁸ Catania, D. 1996. Personal commun. Ichthyology Department, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118.

⁹ Saul, W. 1996. Personal commun. Academy of Natural Sciences, 19th and The Parkway, Philadelphia, PA 19103.

¹⁰ Feeney, R. 1996. Personal commun. Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

¹¹ Jewett, S. 1995. Personal commun. Division of Fishes, Smithsonian Institution, Washington, D.C. 20560.

Girard (1856) described *Platichthys umbrosus* on the basis of a single specimen deposited at the USNM, which was collected at Cape Flattery, Washington, by Lieutenant W. P. Trowbridge. One lot listed in the catalog, USNM 607, bears the collector's name as Trowbridge and a collection date of 1856, and thus the single specimen of this lot appears to have been the one examined by Girard for his original description. From the original description, the specimen is approximately 190 mm TL. Unfortunately, this lot cannot be found and is presumed missing or destroyed.¹¹

Girard was apparently unaware of Ayres' (1855a, 1855b) description of *L. bilineata* (Leviton and Aldrich, 1997). Although Gunther (1862) considered *Platichthys umbrosus* distinct (basing his conclusion on the dried skins identified as *P. umbrosus* taken off Vancouver Island, Canada, and on the descriptions of *L. bilineata* provided by Ayres), later authors have treated *P. umbrosus* as a synonym of *L. bilineata* (Lockington, 1880a, 1880b; Jordan and Gilbert, 1881; Jordan and Evermann, 1898; Norman, 1934; Schmidt, 1950), and the name has not been used at the species level since Lockington's (1879b) misidentification of *Isopsetta isolepis*. *Lepidopsetta polyxystra* n. sp. also ranges south along the east coast of Vancouver Island, the "Inside Passage," to Puget Sound, and larvae of the new species have been recorded from the extreme northwest coast of Vancouver Island. Although *L. bilineata* is present, but uncommon, off the west coast of Vancouver Island, no adults or larvae of *L. polyxystra* n. sp. have been collected off Washington (Cape Flattery and south), despite the intensive survey efforts of the 1995 and 1998 NMFS triennial surveys, during which all captured *Lepidopsetta* were examined. Although the original description is insufficient to refer it to either of these species, the type locality lies well within the known range of *L. bilineata* and outside that of *L. polyxystra* n. sp. and we therefore consider *Platichthys umbrosus* to be a synonym of *L. bilineata*.

Cope's (1873) description of *Pleuronectes perarcuatus*, from a specimen taken somewhere along the eastern Pacific Ocean coast of Alaska, perhaps near Sitka or Unalaska Island, included a comparison with Girard's *Platichthys umbrosus* but not with Ayres's *Platessa bilineata*. Although the holotype is badly damaged, especially about the head, the gill-raker count and structure, as well as presence of at least one supraorbital pore at the dorsal margin of the orbit,⁸ indicate the holotype is *L. bilineata*. The specimen has a high lateral-line pore count at the upper range of counts for *L. bilineata*. The name has been considered synonymous with, or a subspecies of, *L. bilineata* by later authors (Jordan and Gilbert, 1881; Jordan and Goss, 1889; Jordan and Evermann, 1898; Wilimovsky et al., 1967).

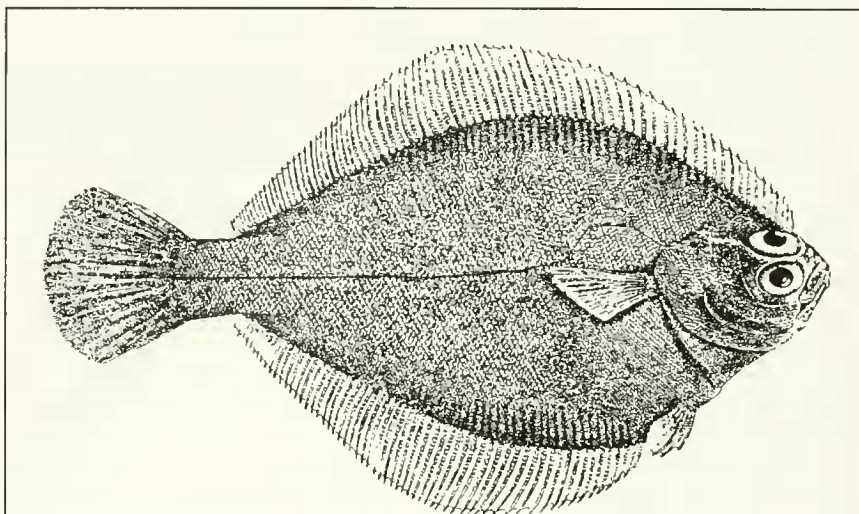


Figure 19

Lepidopsetta mochigarei Snyder, holotype, USNM 68245, 1(174 mm), Japan, Hokkaido, Otaru Market, 1906. After Snyder (1912).

***Lepidopsetta mochigarei* Snyder, 1911**

Ricecake sole

Asabagarei

Figs. 1–2, 7, 19–20; Tables 3–10, 13

Lepidopsetta mochigarei Snyder, 1911:547 (original description, two specimens: holotype by original designation, USNM 68245, male, 174 mm, and "cotype," SU 21430, 145 mm TL, both from the market at Otaru, Hokkaido, Japan).

Lepidopsetta bilineata mochigarei Taranets, 1937:144 (new combination, keys).

Pleuronectes mochigarei Sakamoto, 1984a:99 (new combination, phylogenetics).

Material examined

Adults 27 specimens, 90.7–280.3 mm, including holotype listed above. Japan: CAS-SU 113378, 1(257.5 mm), Bomasiri Shima, off N end of Rebun To., 45°25.5'N, 140°53'E, 22 September 1906; CAS-SU 122548, 1(146.7 mm), Tsugaru Strait/Sea of Japan, between Hakodate, Hokkaido and Ebisu, Sado I., S of Cape Tsiuka, 41°35.8333'N, 140°36.75'E, 16 July 1906; HUMZ 56717, 1(154 mm), Hokkaido, off Kushiro; HUMZ 58576, 1(189 mm), Hokkaido, off Otanoshike; HUMZ 58566, 1(197.5 mm), Otanoshike, off Hokkaido, 20 m; HUMZ 58563, 1(200.5 mm), Otanoshike, off Hokkaido, 20 m; HUMZ 58568, 1(171.5 mm), Otanoshike, off Hokkaido; HUMZ 58567, 1(184 mm), Hokkaido, off Otanoshike; HUMZ 87820, 1(175 mm), Hokkaido, off Muroran, 135 m; HUMZ 80974, 1(190.5 mm), Hokkaido, off Muroran; HUMZ 81056, 1(167.5 mm), Hokkaido, Usujiri, Minamikayabe; HUMZ 90912, 1(142.5 mm), Hokkaido, off Tomakomai, 300 m; HUMZ 64730, 1(116.6 mm), Hokkaido, Funkawan; HUMZ 15505, 1(107.2 mm), Hokkaido, Funka Bay; HUMZ

15456, 1(130.5 mm), Hokkaido, Funka Bay; HUMZ 15506, 1(90.7 mm), Hokkaido, Funka Bay; HUMZ 94034, 1(193.5 mm), Hokkaido, off Tomakomai, 300 m; UBC 58-355, 2(204–240 mm), Japan; USNM 150380, 1(130.6 mm), Hokkaido; USNM 077125, 1(166.1 mm), 104 km S of OseSaki, Albatross Sta. 5067, 35.0972°N, 138.6875°E, 536 m; Russia: USNM 77126, 1(244.2 mm), Gulf of Tartary, off SW coast of Sakhalin I., Albatross Sta. 4999, 47.6389°N, 141.65°E; USNM 77127, 1(247.4 mm), Aniwa Bay, approaching Korsokov, Sakhalin I., 73 m, Albatross Sta. 5008, 46.1306°N, 142.6222°E; USNM 77130, 1(280.3 mm), Gulf of Tartary, off SW coast of Sakhalin I., 57 m, Albatross Sta. 5000, 46.55°N, 142.7083°E; USNM 77128, 1(257 mm), Aniwa Bay, approaching Korsokov, Sakhalin I., 77 m, Albatross Sta. 5007, 46.05°N, 142.5167°E; USNM 77135, 1(246.8 mm), Sakhalin I., off Korsokov Lt., 39–56 m, Albatross Sta. 5010, 46.55°N, 142.725°E.

Diagnosis

Lepidopsetta mochigarei is a species of *Lepidopsetta* with the following combination of characters in adults: total gill rakers on first arch 6–10, on upper arch 1–3; total gill rakers on second arch 7–10; supraorbital pores 1–3; preopercular pores 8–13; lateral-line pores 95–119; sum of scales above and below lateral line 91–108; interorbital narrow; blind-side coloration white, and glossy highlights along myotome margins increasing anteriorly.

Larvae are distinguished from other species of *Lepidopsetta* by having the following combination of characters: body deep, increasing rapidly with development and snout-to-anus length moderate; larvae undergoing notochord flexion at comparatively larger sizes; preflexion pigment pattern with three prominent spots along margin of dorsal finfold and two spots along ventral finfold, three patches along postanal dorsal midline aligned with finfold spots to form slightly offset opposing patches, posteriormost dorsal spot coalescing with a corresponding ventral spot to form a bar; pectoral-fin rays pigmented (Okiyama and Takahashi, 1976; Nagasawa, cited in Okiyama, 1988).

Description of adults

Body ovate, relatively deep, greatest depth 45.5–61.1 (51.7)% SL, scales above lateral line 35–45 scales below

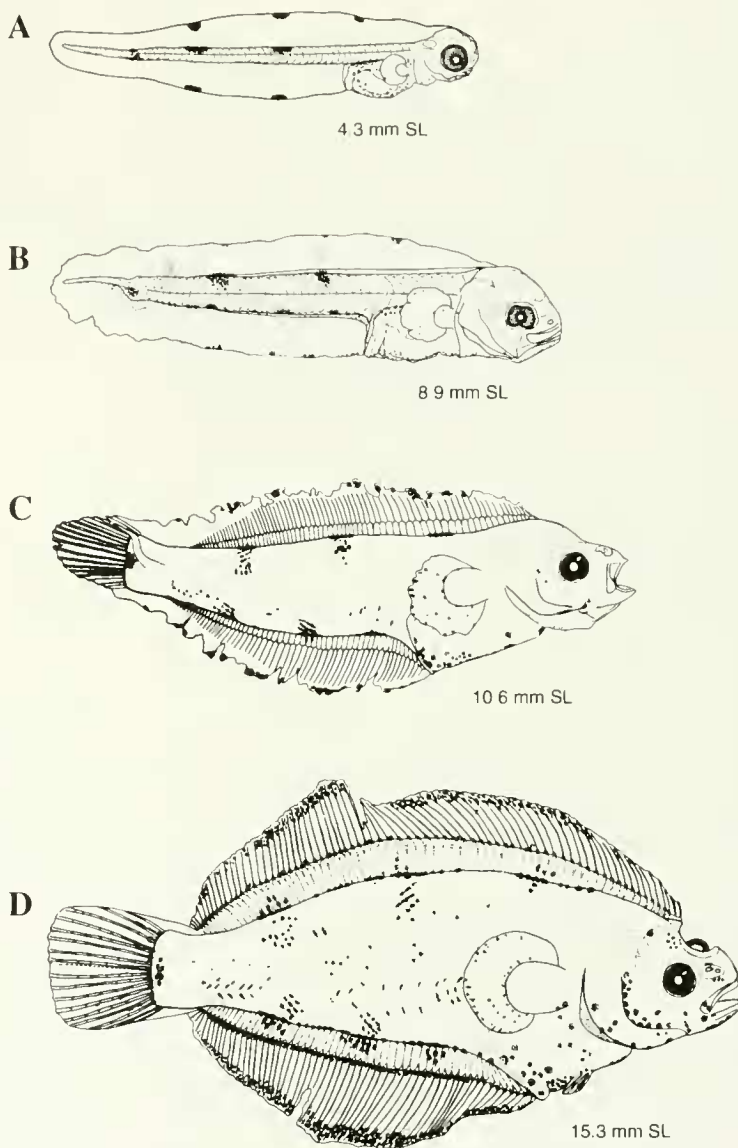


Figure 20

Larvae of *Lepidopsetta mochigarei* Snyder (figures reproduced from Okiyama, 1988): (A) 4.3 mm, Japan Sea (Okiyama and Takahashi, 1976); (B) 8.9 mm, Sea of Japan (Okiyama and Takahashi, 1976); (C) 10.6 mm, Sea of Japan (original illustration of Nagasawa, cited in Okiyama, 1988, locality implied in text); (D) 15.3 mm, Sea of Japan (original illustration of Nagasawa, cited in Okiyama, 1988, locality implied in text).

lateral line 52–67; head relatively short and robust, length 23.3–30.5 (26.2)% SL; dorsal margin of head at dorsal-fin origin nearly linear, snout length 3.3–6.2 (4.3)% SL (12.7–20.2 (16.1)% HL); ocular-side maxilla length 24.6–29.4 (27.2)% HL; blind-side maxilla length 27.3–32.9 (29.7)% HL; ocular-side mandible length 36.6–44.6 (39.7)% HL; teeth 6–10 on ocular-side premaxilla, 23 on blind-side premaxilla and 8–15 on ocular-side dentary, 21–28 on blind-side dentary; gill rakers of first arch broad and robust, 6–10 total, 1–3 on upper arch, 4–7 on lower; gill

rakers of second arch 7–10 total, 1 on upper and 6–9 on lower arch; eyes relatively large, dorsal orbit slightly longer than eye length, orbit length 26.1–34.7 (30.1)% HL, eye length 21.4–30.0 (25.3)% HL; ventral eye length 21.6–31.1 (25.5)% HL; interorbital a narrow ridge, up to 2 scales at narrowest portion, 1.3–4.2 (2.7)% HL; cheek with 10–15 scales, length 28.6–35.0 (31.1)% HL, depth 14.8–25.5 (19.7)% HL; preopercular pores 8–13; ocular-side suborbital pores 22–38; blind-side suborbital pores 10–20; lateral line pores 95–119, lateral-line arch relatively long, 53.7–69.9 (62.7)% HL, its depth 23.8–35.7 (30.9)% its length; both anterior and posterior supratemporal branches relatively short, anterior pores 3–12, posterior pores 6–22; supraorbital canal short, reaching only to the posterior rim of the dorsal orbit at about the insertion of dorsal-fin rays 5–6, pores 1–3; ocular-side pectoral-fin length 12.6–17.4 (14.6)% SL (47.9–60.2 (55.6)% HL); blind-side pectoral-fin length 7.9–11.7 (9.6)% SL (30.3–42.8 (36.5)% HL); ocular-side pelvic-fin length 7.4–11.8 (9.8)% SL (31.8–43.5 (37.4)% HL); dorsal fin with 73–82 rays, height 11.2–14.7 (12.9)% SL, in specimens with 75–81 rays supported by 71–77 pterygiophores, typically 8 or rarely 9 anterior to first neural spine; anal fin with 56–65 rays, in specimens with 56–63 rays supported by 57–61 pterygiophores; caudal peduncle relatively deep, least caudal peduncle depth 9.7–14.0 (11.0)% SL (36.2–50.3 (42.2)% HL; 105.1–172 (124.3)% caudal peduncle length), greatest caudal peduncle depth 12.0–14.6 (13.2)% SL (44.7–56.0 (50.5)% HL); caudal peduncle length 7.8–10.3 (8.9)% SL (27.5–39.4 (34.1)% HL); caudal-fin length 18.8–25.1 (21.2)% SL. Vertebrae 39–42, with 11 precaudal and 28–31 caudal.

Scales on head, pectoral region, and those scattered posteriorly on ocular side slightly rough and having columnar tubercles in larger adults. Small spines present in small adults.

In life, blind side of adults translucent to white with glossy highlights along edges of myotomes (Amaoka et al., 1983, Fig. 220 as *L. bilineata*; Amaoka et al., 1995, Fig. 524 as *Pleuronectes bilineatus*). When preserved, blind side uniform creamy white to yellow-brown. Ocular side brownish with faint yellow highlights around small dark spots near bases of dorsal and anal fins and at midline (Amaoka et al., 1995, Fig. 524).

Remaining description as for genus. Largest specimen examined 280.3 mm (USNM 77130). Maximum size reported 400 mm SL (Sakamoto, 1984b).

Description of juveniles

No juveniles were examined for this study. Juveniles are not described in available literature.

Description of larvae

No larvae were examined in our study. The following description is based on Okiyama and Takahasi (1976, based on 3 specimens of 4.12–8.59 mm) and Pertseva-Ostroumova (1961; number and size of specimens examined not stated).

Snout-to-anus length 32.8–37.0% SL, decreasing with development according to Pertseva-Ostroumova, 1961 (34.2–32.5% SL); body depth 9.0–17.0% SL, increasing with development; head length 15.0–20.0% SL, increasing with development; orbit length 41.0–28.0% HL, decreases with development. Total myomeres 41–43.

Hatching occurring at relatively large sizes, at 3.95–4.48 mm (Yusa, 1958); flexion beginning by 8.9 mm (Fig. B of Okiyama, 1988); postflexion size between 10.6 mm and 15.3 mm (Figs. C and D of Okiyama, 1988); transformation occurring at sizes larger than 15.3 mm (Fig. D of Okiyama, 1988).

Preanal pigment (Fig. 20, based on Okiyama, 1988) present initially along lower jaw, extending ventrally along gut to anus. By flexion, melanophores appearing on pectoral-fin rays; pectoral-fin rays and base not pigmented in all earlier developmental stages; pectoral fin pigmented more heavily than *L. polyxystra* n. sp. by later stages (Pertseva-Ostroumova, 1961).

Postanal pigment of preflexion larvae in prominent patches of melanophores along finfold edges, three along dorsal and two along anal finfold, becoming more dispersed and less prominent with development; three distinct pigment patches along the dorsal midline, anterior patch begins at about myomere 20–22, posterior patch begins at about 33–36, and caudal patch, which aligns with a ventral patch to form a caudal bar, begins in the range of myomeres 40–44; these dorsal midline patches align vertically with the two posteriormost dorsal and both ventral finfold patches; a series of melanophores may occur along the postanal ventral midline (additional descriptions cannot be found in the literature); additional pigment spots above and below the notochord tip.

Distribution

Lepidopsetta mochigarei ranges in the western Pacific Ocean from the east coast of Korea, Yaglin Bay, in the Sea of Japan (Kim and Youn, 1994) to Iturup Island of the Kuril Islands in the southern Okhotsk Sea (Nikiforov et al., 1983), and to the west coast of northern Japan. Larvae have been collected in March along the coast of northern Honshu in the Sea of Japan (Okiyama, 1988).

Habitat

Adults have been collected over the continental shelf; spawning may occur in depths of about 120 m (Okada, 1955).

Life history

Fecundity ranges from 510,000 to 550,000 eggs (Okada, 1955). Spawning eggs are demersal and adherent, about 0.87–0.95 mm in diameter (Yusa, 1958; Pertseva-Ostroumova, 1961); oocytes at maturation stage IV were 0.440–0.655 mm in diameter (Nikiforov et al., 1983). Spawning occurs from December to June in waters around Hokkaido and the southern Kuril Islands (Minami, 1995). Embryonic and larval development to about 5.0 mm has been described by Yusa (1958).

Etymology

The species name *mochigarei* is derived from the Japanese, meaning "rice-cake flounder" (Snyder, 1911), probably a reference to the bright white blind side similar to white rice-cake common in Japan.¹²

Comments

Masutomi and Hamada (1966) described a fossil of *L. mochigarei*. It was subsequently described as the extinct *Chibapsetta dolichurostyli* by Sakamoto and Uyeno (1988).

Because early life history material was not available for examination, descriptions were based on the available literature (Yusa, 1957, 1958; Pertseva-Ostroumova, 1961; Okiyama and Takahashi, 1976; Okiyama, 1988). Several potentially important characters could not be gleaned from the available sources: an anterior pigment spot along the dorsal midline, important in distinguishing *L. bilineata* from *L. polyxystra* n. sp. (Figs. 17C, 17D), is not present in preflexion larvae (Figs. 20A and 20B). Because the sources were different, we needed verification that these figures constitute a series. Although present, the extent of the postanal ventral melanophores, important in distinguishing *Lepidopsetta* from *Psettichthys* in particular as well as from other pleuronectids, is not known. Additional data for morphological characters were also needed for all developmental stages. Larvae of *L. mochigarei* appear more similar to those of *L. bilineata* than *L. polyxystra* n. sp., but they are not sympatric with *L. bilineata*. Based on the present descriptions, larvae of *L. mochigarei* can be distinguished from those of *L. polyxystra* n. sp. by the distinctive vertically aligned dorsal midline and finfold pigment.

Lepidopsetta polyxystra n. sp.

Northern rock sole

Figs. 1–5, 8, 11, 13, 21–24; Tables 2–11, 13–14

Lepidopsetta bilineata var. *umbrosa* Jordan and Evermann, 1898:2643 (in part, Fig. 928).

Lepidopsetta bilineata bilineata Taranetz, 1937:144 (in part, new combination, keys).

Holotype

UW 014826, 1(169.7 mm), Alaska, Aleutian Is., Amchitka I., Constantine Harbor, 19–42 m, 19 August 1955.

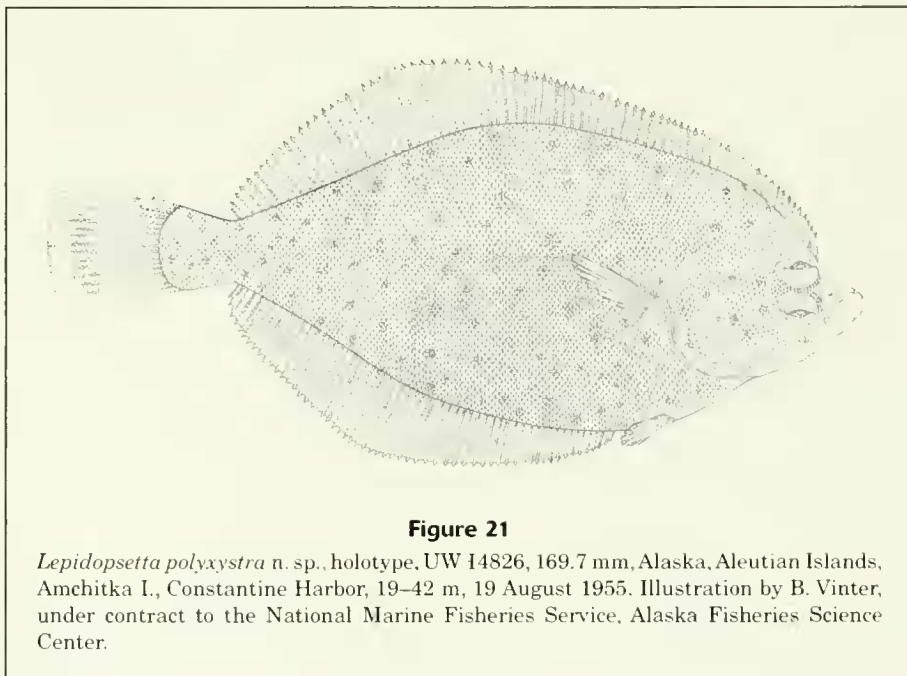


Figure 21

Lepidopsetta polyxystra n. sp., holotype, UW 14826, 169.7 mm, Alaska, Aleutian Islands, Amchitka I., Constantine Harbor, 19–42 m, 19 August 1955. Illustration by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

Material examined

A total of 843 adults and juveniles, including the holotype listed above, was examined. Sixty larvae were examined.

Paratypes

Adults 219 specimens, 26–427.5 mm. Okhotsk Sea: UW 042341 (orig. KIE 1147), 2(105.5–109.5 mm), western Kamchatka, 51°57'N, 156°25'E; UW 042342 (orig. KIE 1149), 3(144.5–195 mm), western Kamchatka, 52°02'N, 155°58'E, 6 June 1992; UW 042343 (orig. KIE 1151), 10(186–247 mm), 52°29'N, 153°40'E, 24 June 1992; KIE 1148, 1(89.5 mm), 51°43'N, 156°04'E, 5 June 1992; Southeast Kamchatka: CAS-SU 122549, 1(112.3 mm), Kamchatka, off Petropavlovsk, 18 June 1906; Bering Sea: KIE 1415, 1(289.5 mm), Bering I., SW of Cape Monati, 54°37'N, 166°31'E, 27 April 1996; KIE 1417, 1(258.5 mm), Bering I., SW of Cape Monati, 54°39'N, 166°29'E, 8 May 1996; KIE 1414, 1(260.5 mm), SW of Cape Monati, 54°40'N, 166°29'E; KIE 1268, 1(338.6 mm), NW of Bering I., 55°34'N, 164°55'E, 7 January 1994; KIE 1418, 1(289 mm), Bering I., SE of Cape Monati, 54.6667°N, 166.8333°E, 9 May 1996; KIE 1416, 1(261 mm), Kamchatka, SW of Cape Northwestern, 55.2833°N, 165.5333°E, 4 May 1996; KIE 1150, 1(238.5 mm), Kamchatka, 56.2333°N, 154.3°E, 18 June 1992; ABL 93-37, 1(193 mm), St. Paul I., Pribilof Is.; ABL 60-15, 1(265 mm), N of Pribilof Is., 58°33'N, 170°12'W, 17 July 1960; UW 041694, 3(150–177), Aleutian Is., NE of Umnak I., 53.44°N, 168.4944°W; SIO 94-164, 9(103–190 mm), Aleutian Is., off Unalaska I., 54°15.1'N, 165°57.6'W, 4 June 94; UW 041199, 1(267 mm), 60.6667°N, 169.65°W, 16 July 1979; UW 041697, 1(245 mm), Bering Sea, N of Unimak I., 55.0213°N, 164.6009°W; CAS 45562, 1(240.8 mm), WNW of Pribilof Is., NE end of Zhenchug Canyon, 58°15.8667°N,

¹² Amaoka, K. 1997. Personal commun. Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, Japan.

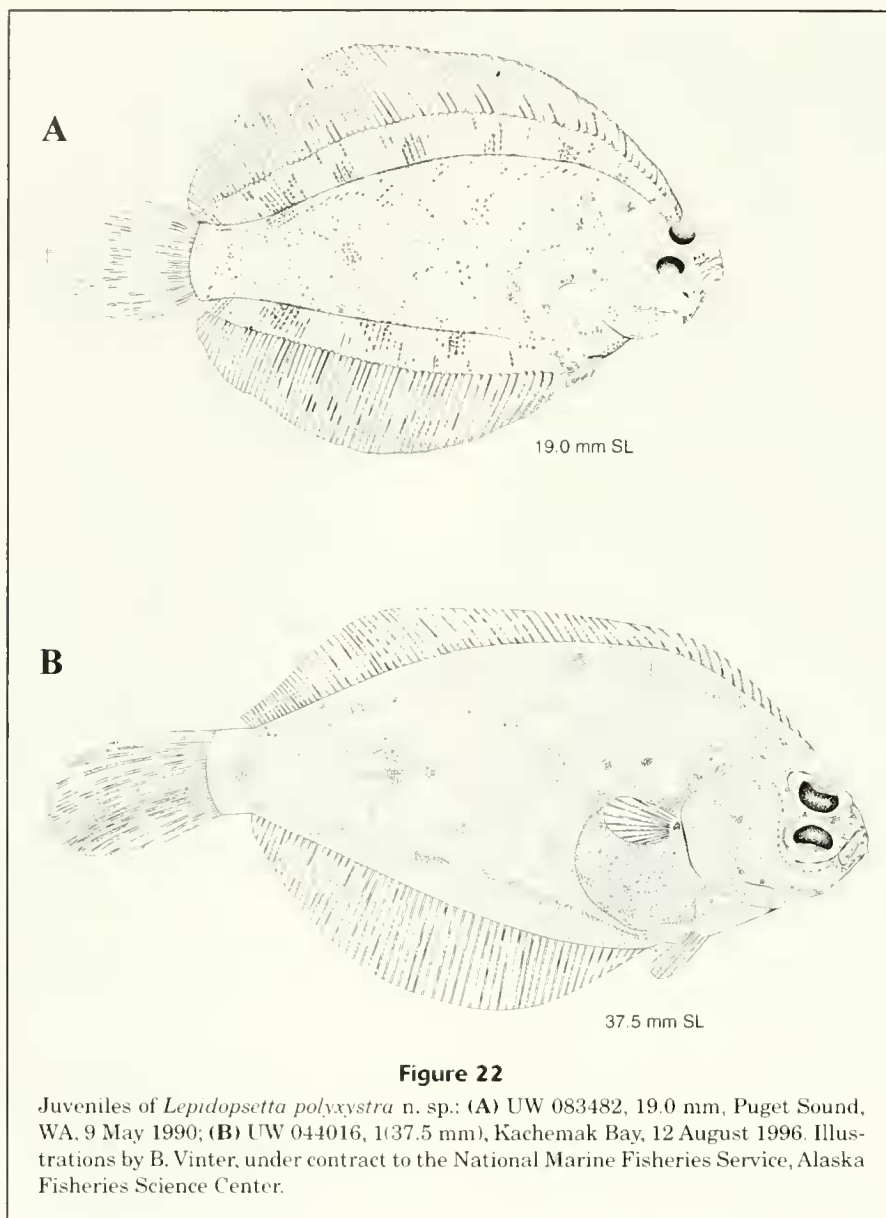


Figure 22

Juveniles of *Lepidopsetta polyxystra* n. sp.: (A) UW 083482, 19.0 mm, Puget Sound, WA, 9 May 1990; (B) UW 044016, 1(37.5 mm), Kachemak Bay, 12 August 1996. Illustrations by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

174°0.3'W, 21 June 79; CAS 45567, 1(272.1 mm), SSW of Pribilof Is., 55°38.8667'N, 168°39.9833'W, 16 June 79; CAS 46676, 1(87.7 mm), Pribilof Is., St. George I., 56°35'N, 169°36'W, 27 July 1977; CAS 47531, 5(181.4–199.4 mm), Aleutian Is., 51°43.9'N, 177°57.8833'W, 10 August 1980; CAS-SU 105731, 5(132.6–182.9 mm), Aleutian Is., Umnak I., off Nikolski, 31 July 1896; USNM 130725, 3(287–310 mm), 40 mi above Port Moller, 8 May 1941; USNM 060905, 1(316.5 mm), Karluk, TT2204, RV *Albatross*; UW 001378, 1(175.5 mm), Unalaska I., 1930; UW 003656, 1(100.5 mm), Alaska Peninsula, Cold Bay, 13 June 1932; UW 013667, 1(208.1 mm), Unimak I., False Pass, 1 July 1957; UW 016609, 1(191 mm), Pribilof Is., St. George I.; UW 025736, 3(28–45.7 mm), Port Moller; UW 016600, 3(83.9–130.9 mm), 58.5833°N, 168.1°W, 4 July 1949; UW 003100, 3(86.7–164.6 mm), Captains Bay, Unalaska I.; UW 10650,

2(81.6–112.8 mm), off Nunivak I., 59°36'N, 167°56'W; UW 14831, 1(83 mm), off Nunivak I., 59.82°N, 169.13°W, 4 July 1949; UW 25760, 1(193 mm), 57.65°N, 167.65°W; UW 25731, 1(178.9 mm), 57.6667°N, 167.2°W, 27 April 1987; UBC 65-39, 1(175 mm), Izembeck Bay, 31 August 1964; UBC 62-565, 2(198–229 mm), 120 km E of St. George I.; UBC 65-730, 2(220–245 mm), 57°45'N, 164°45'W, 16 August 1965; UBC 65-714, 1(160 mm), 57°45'N, 168°45'W, 1 August 1965; UBC 65-729, 1(150 mm), 55°45'N, 162°45'W, 14 August 1965; Gulf of Alaska: ABL 72-74, 6(26–59.3 mm), SE shore of Favorite Channel, 10 November 1972; ABL Uncat, 1(195 mm), Unalaska I., 18 June 1958; 86ABL 62-202, 3(83.5–88 mm), Auke Bay, ca. 17.6 km NW of Juneau, 23 May 1962; ABL 62-199, 1(52.3 mm), 19.2 km NW of Juneau; ABL 64-996, 2(65.6–69.5 mm), Auke Bay, ca. 17.6 km NW of Juneau, 30 April 1964; ABL 67-32,

1(265 mm), Baranof I., Katlian Bay, 19 April 1967; OS 17158, 20(227–315 mm), 55.3323°N, 161.3186°W, 32 m, 3 June 1996; OS 17157, 3(230–262 mm), Aleutian Is., 51.88373°N 179.7202°E, 95 m, 16 July 1997; OS 3497, 1(213 mm), False Pass, Ikatan Bay, 19 June 1956; OS out of 6447, 2(166.1–170.2 mm), 57°10'N, 151°40.5'W, 77 m, 20 September 1978; OS 2157, 1(92 mm), Kodiak I., Shelikof St., mouth of Sturgeon R., 9–10 September 1954; OS 2169, 1(64 mm), Moffet Pt. to Black Hill, 28 May 1957; OS 2173, 1(63.5 mm), Moffet Pt. to Black Hill, 3 June 1957; OS 3979, 1(94.6 mm), Little Port Walter, 8 August 1964; SIO 69-748, 3(51–195 mm) of 7(51–195 mm), Afognak I., Kitoi Bay, 16–21 April 1968; SIO 76-299, 1(270 mm), Kodiak shelf, 56°43'N, 153°22'W, 25 June 1976; SIO 72-227, 1(235 mm), 40 km NW of Juneau, Lynn Canal, 16 February 1963; USNM 130734, 1(254.5 mm), Ivanof Bay, 3 April 1941; USNM 27602, 1(261.8 mm), Kodiak I., 12 July 1880; USNM 27942, 1(260.2 mm), Cook Inlet, Port Chatham; USNM 116332, 2(293–295 mm), Canoe Bay, 17 September–15 October 1940; UW 003854, 1(355 mm), Alitak Bay, Kodiak I., 9 June 1932; UW 040498, 1(195 mm), Prince William Sound, 1989; UW 025740, 1(68.4 mm), Ugak Bay, Kodiak I.; UW 044029, 1(276 mm), 59.5743°N, 151.325°W, 11 m depth, 26 February 1996; UW 044001, 18(52.7–99 mm) [3(30–40 mm) of 18 used for illustration], Prince William Sound; UBC 59-485, 2(71–116.2 mm), Chief Cove, Spiridon Bay; UBC 65-572, 1(74 mm), Boussole Bay, 29 June 1965; UBC 63-174, 1(290 mm), Prince William Sound, off Cordova; UBC 65-148, 1(205 mm), W of Chirikof I., 3 August 1964. British Columbia: SIO 63-206-64B, 1(97 mm), Vancouver I., Stanley Park at Lumberman's Arch, 15 March 1963; UBC 56-83, 3(83.5–121.3 mm), Strait of Georgia, off Saturna I.; UBC 62-874, 1(120 mm), off Sooke, 20 June 1962; Puget Sound: OS 3565, 1(224 mm), Puget Sound, 3 February 1943; UW 041078, 2(126–144 mm), Nisqually Reach, 25 February 1949; UW 004411, 1(36 mm), Edmonds, 1 June 1938; UW 000203, 1(45.9 mm), Lopez I., 12 August 1929; UW 041678, 1(67.2 mm), San Juan Islands, East Sound, 11 December 1964; UW 041675, 3(53.7–166.5 mm), Port Townsend Bay, 5 December 1978–5 January 1979; UW 018096, 1(182.4 mm), Bellingham Bay, Chuckanut Bay, May 1964; UW 044014, 29(121–223 mm), 47°19.48'N,

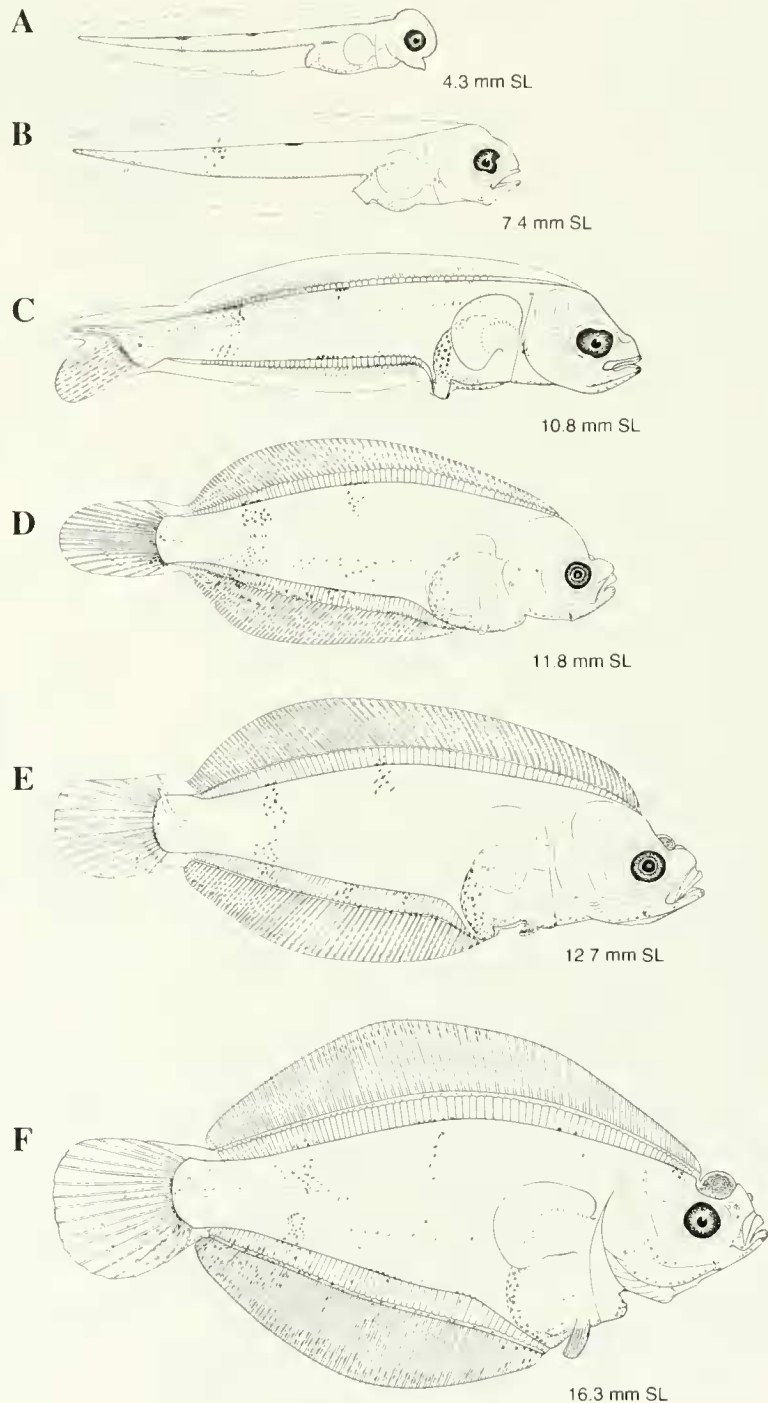


Figure 23

Larvae of *Lepidopsetta polyxystra* n. sp.: (A) UW 069346, 4.3 mm, Gulf of Alaska, 30 March 1978 (Matarese et al., 1989); (B) UW 083455, 7.4 mm, Gulf of Alaska, 15 May 1979 (Matarese et al., 1989); (C) UW 083446, 10.8 mm, Bering Sea, 26 July 1971 (Matarese et al., 1989); (D) UW 063735, 11.8 mm, Gulf of Alaska, 25 May 1985; (E) UW 083453, 12.7 mm, Gulf of Alaska, 24 June 1978; (F) UW 083454, 16.3 mm, Gulf of Alaska, 24 June 1978 (Matarese et al., 1989). Illustrations by B. Vinter, under contract to the National Marine Fisheries Service, Alaska Fisheries Science Center.

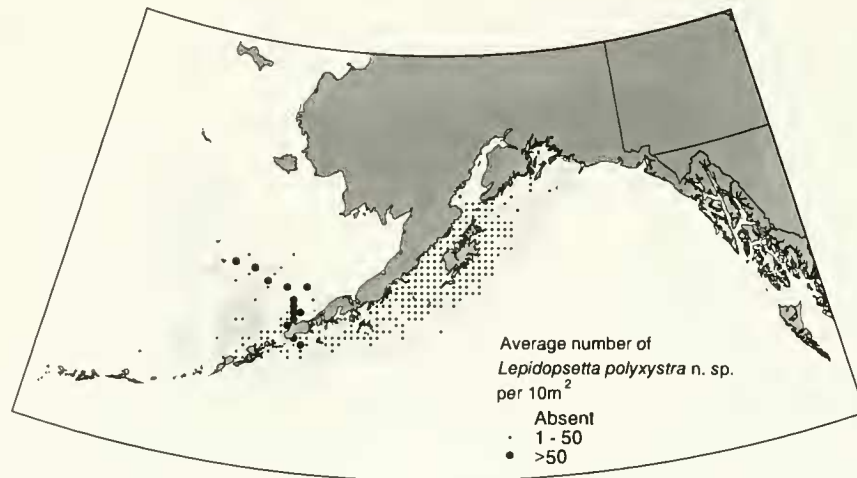


Figure 24

Distribution and density (average number per 10 m²) of *Lepidopsetta polyxystra* n. sp. in the Gulf of Alaska and Bering Sea, 1972–1994.

122°33.8'W, 10 May 1996; UW 044007, 9(135–200 mm), Nisqually, 47°9.47'N, 122°40.16'W, 16 May 1996.

Larvae 18 specimens, 3.3–18.6 mm, examined. Bering Sea: UW 083475, 1(3.7 mm), 55°47.0'N, 165°59.0'W, 0–117 m depth, bongo net, 19 April 1991; Gulf of Alaska: UW 083456, 1(3.3 mm), 58°22.0'N, 150°06.0'W, 0–52 m depth, bongo net, 9 April 1991; UW 083479, 1(11.2 mm), 57°19.0'N, 156°09.0'W, 0–100 m depth, bongo net, 4 June 1990; UW 083457, 1(4.2 mm), 56°30.0'N, 157°00.2'W, 0–43 m depth, bongo net, 24 April 1991; UW 083476, 1(5.2 mm), 56°54.3'N, 156°15.3'W, 0–100 m depth, bongo net, 9 May 1992; UW 083461, 1(6.4 mm), 56°46.1'N, 156°47.9'W, 0–47 m depth, bongo net, 24 May 1991; UW 083472, 1(7.2 mm), 56°46.2'N, 156°33.6'W, 0–99 m depth, bongo net (333 mesh), 13 May 1992; UW 083471, 1(8.8 mm), 56°46.2'N, 156°33.6'W, 0–99 m depth, bongo net, 13 May 1992; UW 083478, 2 of 10 (10.0–10.7 mm), 56°56.7'N, 154°43.2'W, 0–42 m depth, bongo net, 5 June 1990; UW 083481, 2(13.6–14.2 mm), 56°54.0'N, 156°29.5'W, 0–84 m depth, bongo net, 3 June 1990; UW 083477, 1(5.7 mm), 55°57.0'N, 158°33.1'W, 0–100 m depth, bongo net, 21 May 1991; UW 083480, 2(12.4–12.6 mm), 55°39.1'N, 156°3.4'W, 0–100 m depth, bongo net, 31 May 1990; UW 083451, 1(17.8 mm), 55°18.1'N, 160°12.0'W, 0–115 m depth, Methot net, 24 July 1991; UW 083450, 1(15.3 mm), 54°39.2'N, 159°23.0'W, 0–54 m depth, Methot net, 29 July 1991; UW 083452, 1(18.6 mm), 54°36.2'N, 162°16.2'W, 0–87 m depth, Methot net, 30 July 1991.

Other material examined

Adults 629 adults and juveniles. Bering Sea: UW 044023, 6(173–292 mm), 60.6869°N, 175.4609°W, 11 July 1995; UW 044020, 2(331–368.5 mm), 58.45°N, 174.33°W; UW 044003, 2(226–249 mm), 58.12°N, 168.43°W; UW 041699, 1(108 mm), 58.66°N, 159.47°W; Gulf of Alaska: UW 044015, 307(18.2–190 mm), Kachemak Bay; UW 044016, 1(37.5

mm), Kachemak Bay; UW 044018, 54(26–90 mm), Kachemak Bay; SIO 76-300, 3(161–200 mm) of 28(145–280 mm), Kodiak shelf, 57°40'N, 150°37'W, 15 March 1963; ABL 68-505, 2(128–140 mm) of 15(15–140 mm) examined, Glacier Bay, 8 August 1968; UW 025735, 2(35.8–61.8 mm), "6/10/83, Sta. 14, Haul 52"; UW 04321, 1(230 mm), Fishing Vessel *Sulak*, Cruise 436, Robin Scheid; UW 002688, 83(56–107 mm), Shumagin Is., Baralof Bay, 27 June 1931; UW 002032, 30(75–137 mm), Yakutat Bay, 21 June 1932; UW 041674, 11(67.5–139 mm), Alexander Archipelago, off Wrangell I., 1 December 1931; UW 003841, 13(72–99 mm), Yakutat Bay, 21 June 1932; UW 004004, 7(77–100 mm), Yakutat Bay, 21 June 1932; UW 005047, 6(97–120 mm), Alitak Bay, 9 June 1932; UW 041681, 1(119.5 mm), Prince William Sound, 1989; UW 002069, 8(106–157.3 mm), Cold Bay, 6–26 May 1932; UW 022413, 5 cleared and stained of 14(53–110 mm), Adak I., Aleutian Is.; UW 040265, 16(159–350 mm), 54.0389°N, 165.8153°W; UW 003913, 5(113.4–167 mm), Prince William Sound, Orca Inlet, 2 April 1935; UW 044012, 6(275–384 mm), 56.5°N, 153.5°W, Bonaduh; UW 020658, 7(56.1–135.7 mm), Kodiak I., Ugak Bay; UW 025763, 1(139.7 mm), off Amchitka I.; UW 040263, 3(214–255 mm), 54°N, 160.74°W. British Columbia: UBC out of 61-609, 3(44.8–56.6 mm), Bute Inlet; UBC out of 60-416, 6(181–230 mm), Queen Charlotte Is., Gillat Arm; UBC out of 62-93, 7(75–111 mm), Nass Bay; UBC out of 61-674, 7(64–81 mm), Dean Channel, off Nescall Bay. Washington, Oregon, and California: UW 041673, 5(68–110.5 mm), San Juan Is., East Sound, 3 March 1937; UW 047270, 6(60–240 mm), Puget Sound, Port Townsend Bay; CAS 19305, 1(246.5 mm), San Francisco (see comments).

Larvae 42 specimens (4.2–20.0 mm) examined: Bering Sea: UW 083446, 1(10.8 mm), 57°30.0'N, 169°30.0'W, depth unknown, bongo net, 26 July 1971; UW 083447, 1(4.5 mm), 54°01.3'N, 166°33.9'W, 0–100 m depth, bongo net, 25 April 1993; Western Gulf of Alaska: UW 083448, 1(15.1 mm),

55°17.7'N, 160°11.7'W, 0–115 m depth, Methot net, 24 July 1991; UW 083449, 1(15.3 mm), 54°39.2'N, 159°23.0'W, 0–54 m depth, Methot net, 29 July 1991; UW 071740, 1(12.0 mm; 11.0 mm as measured in this study), 55°38.6'N, 153°30.1'W, 0–102 m depth, bongo net, 31 May 1990; UW 071752, 1(10.0 mm; 9.4 mm as measured in this study), 55°31.6'N, 156°16.3'W, 0–100 m depth, bongo net, 31 May 1990; UW 072106, 1 of 2(17.1 mm), 56°46.2'N, 156°33.6'W, 0–100 m depth, bongo net, 3 June 1990; Gulf of Alaska: UW 069346, 1(4.3 mm) of 9, 58°22.0'N, 150°12.8'W, 0–47 m depth, bongo net, 30 March 1978; UW 083453, 1(12.7 mm), 56°41.9'N, 154°33.2'W, 0–16 m depth, bongo net, 24 June 1978; UW 083454, 1(16.3 mm), 57°19.5'N, 152°23.9'W, 0–48 m depth, bongo net, 24 June 1978; UW 083455, 1(7.4 mm), 56°23.7'N, 155°45.0'W, 0–79 m depth, bongo net, 15 May 1979; UW 063735, 1 of 12 (11.8 mm), 56°35.1'N, 153°43.6'W, 0–70 m depth, bongo net, 25 May 1985; UW 072459, 1 of 10 (9.4 mm), 57°10.7'N, 155°12.9'W, 0–100 m depth, bongo net, 5 June 1990; UW 072497, 6 of 10 (7.4–12.6 mm), 56°56.7'N, 154°43.2'W, 0–42 m depth, bongo net, 5 June 1990; UW 072502, 4 of 9 (7.3–10.3 mm), 56°49.4'N, 154°30.3'W, 0–60 m depth, bongo net, 5 June 1990; UW 072511, 1(12.2 mm), 57°28.6'N, 154°42.4'W, 0–60 m depth, bongo net, 5 June 1990; UW 072546, 1(8.1 mm), 57°40.6'N, 155°10.5'W, 0–287 m depth, bongo net, 6 June 1990; UW 083458, 1(6.8 mm), 57°15.6'N, 155°55.4'W, depth unknown, Mocness net, 14 May 1991; UW 083460, 1(6.4 mm), 56°16.4'N, 158°04.9'W, 0–64 m depth, bongo net, 22 May 1991; UW 083463, 1(4.2 mm), 57°52.3'N, 155°0.1'W, 0–82 m depth, bongo net, 7 April 1992; UW 083464, 1(5.0 mm), 57°42.2'N, 154°47.3'W, 0–219 m depth, bongo net, 7 April 1992; UW 083465, 1(5.5 mm), 57°16.5'N, 155°55.0'W, 0–100 m depth, bongo net, 8 May 1992; UW 083466, 1(5.8 mm), 56°54.3'N, 156°15.3'W, 0–100 m depth, bongo net, 9 May 1992; UW 083467, 3(4.6–6.0 mm), 56°51.8'N, 156°21.4'W, 0–99 m depth, bongo net, 9 May 1992; UW 083468, 1(6.1 mm), 56°53.3'N, 156°23.9'W, 0–102 m depth, bongo net, 9 May 1992; UW 083469, 1(8.5 mm), 56°42.2'N, 156°32.3'W, 0–100 m depth, bongo net, 13 May 1992; UW 083470, 1(6.7 mm), 56°44.4'N, 156°28.7'W, 0–102 m depth, bongo net, 13 May 1992; UW 083473, 1(7.6 mm), 56°09.4'N, 157°14.3'W, 0–101 m depth, bongo net, 22 May 1992; UW 083474, 1(7.5 mm), 56°40.6'N, 155°10.4'W, 0–59 m depth, bongo net, 15 May 1992; UW 083482, 2(19.0–20.0 mm), 47°34.15'N, 122°32.30'W, 0 m depth, dip net, 9 May 1990.

Diagnosis

Lepidopsetta polyxystra is a species of *Lepidopsetta* with the following combination of characters in adults: total gill rakers on first arch 9–14, on upper arch 2–6; total gill rakers on second arch 8–14; supraorbital pores 1–3, rarely 4–7; preopercular pores 5–8; lateral-line pores 76–100; sum of scales above and below lateral line 66–96; interorbital wide; blind side coloration in life creamy, without glossy highlights along margins of myotomes.

Larvae are distinguished from other species of *Lepidopsetta* by the following characters: body slender; snout-to-anus length long; larvae undergo hatching, flexion, and transformation at comparatively larger sizes; preflexion pigment pattern with light pigmentation along finfolds,

limited mainly to the ventral finfold, and two pigment spots along the dorsal midline (the posteriormost aligning with a ventral patch forming a bar), a series of small melanophores extending from just posterior to the anus to just beyond the postanal bar (about 2/3 body); and flexion pigment pattern with a single bar located on the postanal body; pectoral-fin rays unpigmented.

Description of adults

Body ovate, greatest depth 41.2–58.9 (49.0)% SL, scales above lateral line 27–40, scales below lateral line 38–59; head relatively acute, length 21.8–31.5 (27.2)% SL; dorsal margin of head at dorsal-fin origin slightly concave, snout length 3.1–5.7 (4.4)% SL (12.1–20.1 (16.0)% HL); ocular-side maxilla length 20.4–31.5 (26.3)% HL; blind-side maxilla length 22.2–35.7 (28.7)% HL; ocular-side mandible length 34.4–50.0 (40.7)% HL; teeth 4–5 on ocular-side premaxilla, 23–24 on blind-side premaxilla and 8–9 on ocular-side dentary, 20–24 on blind-side dentary; gill rakers of first arch relatively slender, 9–14 total, 3–6 on upper arch, 6–9 on lower arch; gill rakers of second arch 8–14 total with 0–4 on upper and 7–13 on lower arch; dorsal orbit length often with posteriorly elongate rim and much longer than eye length, orbit length 22.2–32.9 (28.1)% HL, dorsal eye length 18.5–32.9 (23.0)% HL; ventral eye length 17.2–31.1 (24.2)% SL; interorbital wide, up to 5 scales at narrowest portion, 2.5–6.6 (4.4)% HL; cheek with 7–12 scales, length 26.7–38.5 (32.5)% HL, depth 13.6–22.7 (18.7)% HL; preopercular pores 5–8; ocular-side suborbital pores 13–29; blind-side suborbital pores 8–14; lateral line pores 76–100, lateral-line arch length 26.1–64.5 (52.3)% HL, its depth 26.3–38.2 (31.7)% its length; both anterior and posterior supratemporal branches relatively long, anterior pores 3–15, posterior pores 10–35; supraorbital canal short, reaching only to the posterior rim of the dorsal orbit at about the insertion of dorsal-fin rays 5–6, pores 1–3, rarely 4–7; ocular-side pectoral-fin length 10.7–18.2 (14.7)% SL (38.3–70.4 (53.9)% HL); blind-side pectoral-fin length 6.6–12.7 (10.2)% SL (24.2–49.6 (37.4)% HL); ocular-side pelvic-fin length 7.8–12.2 (9.9)% SL (27.6–45.9 (36.6)% HL); dorsal fin with 64–83 rays, height 10.2–16.6 (13.5)% SL, in specimens with 69–80 rays supported by 68–78 pterygiophores, typically 9 or rarely 8 anterior to first neural spine; anal fin with 49–64 rays, in specimens with 55–61 rays supported by 53–63 pterygiophores; caudal peduncle relatively slender, least depth 9.4–13.1 (10.9)% SL (32.2–48.8 (40.2)% HL, 101.2–144.2 (123)% caudal peduncle length), greatest depth 10.1–16.9 (12.3)% SL (38.1–57.7 (45.2)% HL); caudal peduncle length 7.0–10.1 (8.9)% SL (27.6–42.0 (32.7)% HL); caudal-fin length 17.8–29.1 (22.7)% SL. Vertebrae 39–41, with 10–11 precaudal and 29–30 caudal.

Scales around head and those scattered posteriorly on ocular side very rough, with columnar tubercles in large adults; strong spines in small adults and juveniles. Urogenital flap unpigmented or lightly pigmented in 23–80 mm juveniles.

In life, blind side in moderate to large adults creamy white, skin opaque (Amaoka et al., 1995, Fig. 525); in juveniles, blind side nearly completely translucent, with small, white glossy areas on head. When preserved, blind side of all individuals uniform creamy white to yellow-brown. Ocular

side slightly less green than that of congeneric in Puget Sound, often with faint yellow highlights around darker spots near bases of dorsal and anal fins and at midline.

Remaining description as for genus. Largest specimen examined 340 mm (427.5 mm TL) (UW 040265). Maximum size reported 588 mm (Fadeev, 1965) to 690 mm TL.⁶

Description of juveniles

Individuals of about 20 mm collected in water column (one 19.0-mm individual examined, UW 083482, not completely transformed; see comments); lateral line and pectoral-fin rays undeveloped; body pigmentation increasing throughout; bars and patches of postflexion larval pigmentation pattern visible; urogenital papilla light or speckled with an unpigmented tip. Eye length smaller, mouth larger, body deeper, gill-raker counts on lower arch higher, distance from pelvic-fin origin to anal-fin origin shorter, expanded anteriormost anal-fin pterygiophore less developed (not protruding beyond body wall in our material) than in similar-size *L. bilineata*.

By 35 mm, many individuals collected near bottom. Post-settlement juveniles (Fig. 22B) as developed as similar-size *L. bilineata*: increased body pigmentation giving juveniles a darker appearance (obscuring urogenital papillae pigment), rays of paired and median fins formed, lateral line formed, supraorbital pores present, expanded anteriormost anal-fin pterygiophore strongly developed.

Description of larvae

Snout-to-anus length 32.1–39.3% SL, remaining constant during development; body depth 3.8–28.5% SL, increasing with development, sharply increasing after flexion; head length 11.6–26.7% SL, increasing with development; snout length 22.8–24.7% HL, remaining constant during development; orbit length 51.8–20.9% HL, decreasing with development (Table 2). Total myomeres 38–42.

Larvae hatching at greater than 3.0 mm (3.6–4.0 mm, Pertseva-Ostroumova, 1961); yolk absorbed by 3.3–4.2 mm. Preflexion larvae ranging in size from 4.2 to 6.2 mm; flexion larvae, 6.2–12.6 mm; postflexion larvae, 12.2–18.6 mm. Transformation occurring at sizes as small as 15.0 mm; post-settlement stage usually not complete by 20.0 mm (Table 13).

Head pigment present initially along lower jaw and underside of chin (Fig. 23); increasing with development to snout, upper jaw, and isthmus. Pigment ventrally along gut and dorsally on anus; by flexion a distinct patch of melanophores along posterior edge of gut; pigment increasing laterally with development.

Postanal pigment light along the anal finfold, melanophores absent on dorsal finfold (Fig. 23); two pigment patches along the dorsal midline, anterior patch beginning about midbody at myomere 18–20, posterior patch beginning about myomere 30, posterior patch aligning with a ventral patch forming a postanal bar; series of melanophores along the ventral body midline beginning just posterior to the anus, extending to just beyond the postanal bar (about 2/3 body length); a few melanophores on caudal peduncle and above and below the notochord tip.

Distribution (Figs. 8, 11, 13, 24)

Ranging from the northern coast of Hokkaido throughout the Kuril Islands and the Okhotsk Sea of the western North Pacific, through the Bering Sea, from the Gulf of Anadyr¹³ to off St. Lawrence Island (Allen and Smith, 1988), to Puget Sound, Washington, in the eastern North Pacific. Large concentrations have been reported from the west and southeast of the Kamchatka Peninsula, where it once composed 90% of the fisheries catches of pleuronectids (Shubnikov and Lisovenko, 1964), and from the south-eastern Bering Sea. Minami and Nakamura (1978) also reported a single specimen of *L. bilineata* (= *L. polyxystra* n. sp. based on distribution) among many *L. mochigarei* from Wakasa Bay, Japan (ca. 35.7°N, 135.5°E); this specimen could not be located.¹⁴ Larvae have been collected from Puget Sound, the east coast and northern tip of Vancouver Island, Hecate Strait, and north along the coasts of Alaska into the Bering Sea. According to Okiyama (1988), larvae occur along the coast of the Kuril Islands, the coast of Kamchatka, and into the Bering Sea.

The recorded locality of one adult (CAS 19305) from San Francisco Bay, over 1200 km south of the nearest verified capture in Puget Sound, is questionable. Although no evidence from catalog records⁸ indicates that the specimen had been misplaced, the specimen was collected in 1888 and has an original catalog number from the Indiana University collection. Its morphology and meristics are distinctively that of more northerly populations.

Habitat

Lepidopsetta collected in the eastern Bering Sea are most commonly associated with sand, and least with "sand and mud," when compared with all other measured substrate types in the Bering Sea, including combinations of sand, gravel, and mud.¹⁵ The maximum depth of collection was 246 m.¹⁶ During the 22-year ichthyoplankton sampling period (all previously unidentified pleuronectid larvae were re-examined, thus providing the only historic distributional records for larvae of *L. polyxystra* n. sp.), larvae were common in spring surveys conducted in the Gulf of Alaska and Bering Sea, when they first appear in March collections; largest catches have been taken in May.

¹³ Kessler, D. 1997. Personal commun. Under contract to Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

¹⁴ Saruwatari, T. 1997. Personal commun. Ocean Research Institute, University of Tokyo, Tokyo, Japan. Shinohara, G. 1997. Personal commun. Fish Section, Department of Zoology, National Science Museum (Natural History), Hunkunin-cho, Shinjuku-ku, Tokyo, Japan.

¹⁵ McConnaughey, R. 1997. Personal commun. Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

¹⁶ Resource Assessment and Conservation Engineering (RACE) Division. 1998. Unpubl. data from the RACE database, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Highest densities of larvae occur in the Bering Sea (Fig. 24), compared with the western Gulf of Alaska.

Life history

Lepidopsetta collected from the eastern Bering Sea and Sakhalin Island, presumed to be *L. polyxystra* n. sp., fed primarily on polychaetes and other marine worms; molluscs (Skalkin, 1959, 1963; Lang et al., 1995) or fishes, primarily *Ammodytes hexapterus* in depths >50 m (Lang et al., 1995), were a second significant component of the diet. Feeding took place primarily from May to September, falling to low levels during the winter (Shubnikov and Lisovenko, 1964) when spawning occurs (Fadeev, 1965). Spawning occurs in areas with good water circulation over hard bottoms of sand with gravel and peaks from early March to mid-April in waters off Kamchatka, possibly occurring as late as mid-June in the western Pacific (Pertseva-Ostroumova, 1961). Fecundity ranges from 151,700 to 404,200 eggs (Fadeev, 1965). Life history including spawning and development was discussed by Pertseva-Ostroumova (1961, as *L. bilineata bilineata*) and larval development was described by Okiyama (1988, as *L. bilineata*).

The Washington Department of Fisheries reported *Lepidopsetta* from late December through early March in sandy gravel of upper intertidal beaches at several sites in central and southern Puget Sound (Penttila, 1995). In January 1991, one beach site on the south shore of Dana Passage (the center of a relatively large area of documented *Lepidopsetta* spawning) was the source of six batches of field-collected spawned eggs (each about 1 mm in diameter) that were subsequently reared through hatching. We identified the reared larvae as *L. polyxystra* n. sp. Egg batches ranged in size from 40 to several hundred eggs and were incubated over about 14 days with ambient central Puget Sound water (about 9.0°C³). Larvae hatched between 4 and 5 mm and had yellow pigmentation associated with the melanophores. For additional early life history information, see generic account.

The maximum recorded age for female *L. polyxystra* n. sp. captured in the Bering Sea is 18 yr at 49 cm FL, and for males is 17 yr at 40 cm FL (Alton and Sample¹⁷). The gills of adults from the Gulf of Alaska have been found to be heavily infested with copepod parasites *Nectobranchia indivisa*, and *Naobranchia occidentalis*, previously recorded in *Lepidopsetta* by Kabata (1988). For both parasites, *L. polyxystra* n. sp. was significantly more heavily infested than *L. bilineata*.⁷ The parasites *Acanthochondria vancouverensis* and *Haemobophes* sp. were also recorded.

Etymology

The specific name *polyxystra* is derived from the Greek *poly*, meaning many, and *xystrus*, meaning raker, referring

to the gill rakers being more numerous than those of congeneric species.

Comments

Under the name of *L. bilineata*, *L. polyxystra* n. sp. has been the subject of many studies. Work on specimens collected north of the extreme southeastern Bering Sea and west of the eastern Aleutian Islands in the western North Pacific may be presumed to be based on *L. polyxystra* n. sp. However, all studies conducted on specimens from the Gulf of Alaska into Puget Sound, regions of extensive overlap in the distributions of *L. polyxystra* n. sp. and *L. bilineata*, should be considered applicable at the generic level only, unless voucher specimens were collected and can be verified.

According to Pertseva-Ostroumova (1961), juveniles as small as 20 mm SL have been collected on the bottom. However, the species exhibits much plasticity in settling size, with specimens much greater than 20 mm SL routinely collected in plankton nets.

A widely published illustration identified as *L. bilineata* is based on a specimen of *L. polyxystra* n. sp. taken off Kodiak Island, Alaska ("St. Paul, Kodiak," USNM 27602), now badly damaged. First published in Goode (1884), it was subsequently reprinted in Jordan and Goss (1889), Jordan and Evermann (1900), Jordan and Starks (1906), and Evermann and Goldsborough (1907) among other publications.

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¹⁷ Alton, M. A., and T. Sample. 1976. Rock sole (family Pleuronectidae). In Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975 (W. T. Pereyra, J. E. Reeves, and R. G. Bakkala), p. 461–474. Northwest and Alaska Fish. Center Proc. Rep., Seattle, WA.

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Appendix Table 1

Summary of Alaska Fisheries Science Center cruises with positive tows for larvae of *Lepidopsetta* (1971–72, 1977–94). Cruises in boldface were not used in calculations of mean density. BS = Bering Sea; GA = Gulf of Alaska; WA = Washington. Bongo = bongo net of 60 cm diameter, 0.505-mm mesh (larvae were occasionally collected using alternative frame sizes, including 20-cm net diameter and 0.333-mm mesh, but these collections were not used for abundance calculations); Meth = Methot trawl net of 5-m² frame (2 × 3 mm oval mesh); Tuck = Tucker trawl net of 1-m frame and 0.505-mm mesh.

Year	Cruises	Region	Month	Gear ¹	Total stations	Total occurrences	
						<i>L. polyxystra</i> n. sp.	<i>L. bilineata</i>
1971	4DE71	BS	Jul–Aug	bongo	10	8²	0
1972	2KE72	GA	Apr–May	bongo	67	27	0
1977	MF77B-5,6	BS	Apr–May	bongo	75	35	0
	9SEI77	GA	Jul	bongo	99	0	1²
1978	4DI78	GA	Mar–Apr	bongo, Tuck	225	80	0
	2MF78	GA	Jun–Jul	bongo, Tuck	267	41	66
	3MF78	GA	Sep	bongo	26	1	1
	4MF78	GA	Sep–Oct	bongo	66	2	0
	5MF78	GA	Oct–Nov	bongo	19	0	1
1979	1PO79	GA	Sep	bongo	18	0	1
	3MF79	BS	Jun–Jul	bongo, Tuck	271	35	0
	5TK79	GA	May	bongo	58	15	3
1980	1MF80	BS	Jan–Feb	bongo	8	2²	0
1981	1PO81	WA	May–Jun	bongo	131	0	1
	1SH81	GA	Mar	bongo	131	4	0
	2MF81	GA	Mar–Apr	bongo	89	1	0
	2SH81	GA	Apr	bongo	60	31	2
	3MF81	GA	Apr–May	bongo	79	37	2
	3SH81	GA	May	bongo	57	37	10
	4MF81	GA	May	bongo	80	52	8
1982	1DA82	GA	Apr	bongo	83	20	0
	2DA82	GA	May	bongo	62	29	1
1983	1CH83	GA	May	bongo	70	19	5
	1EQ83	WA	Apr–May	bongo	124	0	1
1984	1SH84	GA	Apr–May	bongo	157	22	1
1985	1PO85	GA	Mar–Apr	bongo	154	37	0
	2MF85	GA	May	bongo	62	4	0
	2PO85	GA	May–Jun	bongo	189	52	17
1986	1GI86	GA	Apr	bongo	149	53	0
	1MF86	GA	Apr	bongo	80	4	0
	2MF86	GA	May	bongo	107	53	0
1987	1BB87	GA	Mar–Apr	bongo	117	12	1
	2MF87	GA	Apr	bongo	142	9	0
	3MF87	GA	May	bongo	60	14	8
1988	1DN88	BS and GA	Mar–May	bongo	203	17	0
	1MF88	GA	Apr	bongo, Tuck	196	51	0
	2MF88	GA	Apr–May	bongo, Meth, Tuck	84	41	1
	3MF88	GA	May	bongo	13	2	0
	4MF88	GA	May–Jun	bongo, Meth, Tuck	209	69	75
1989	1MF89	GA	Apr	bongo, Tuck	140	21	0
	2MF89	GA	Apr–May	bongo, Tuck	107	55	1
	3MF89	GA	May	bongo, Meth, Tuck	221	127	2
	4MF89	GA	May–Jun	Tuck	95	87	9

Continued

Appendix Table 1 (continued)

Year	Cruises	Region	Month	Gear ¹	Total stations	Total occurrences	
						<i>L. polyxystra</i> n. sp.	<i>L. bilineata</i>
1990	1MF90	GA	Apr	bongo	107	17	0
	2MF90	GA	May	bongo,Tuck	92	52	2
	3MF90	GA	May	bongo	17	9	0
	4MF90	GA	May-Jun	bongo	130	83	21
1991	1MF91	GA	Apr	bongo,Tuck	98	5	0
	2MF91	GA	Apr	bongo,Tuck	156	24	0
	3MF91	GA	May	bongo	119	28	0
	4MF91	GA	May	bongo	98	19	8
	5MF91	WGA	July	Meth	62	40	12
1992	1MF92	GA	Apr	bongo,Tuck	103	7	0
	1MM92	BS and GA	Jul	Meth	11	3	2
	3MF92	GA	May	bongo,Tuck	188	59	7
	4MF92	GA	May	bongo, Meth,Tuck	154	46	31
1993	2MF93	GA	Apr	bongo, Meth,Tuck	135	12	0
	3MF93	BS	Apr	bongo,Tuck	135	21	0
	4MF93	GA	May	bongo, Meth,Tuck	168	44	7
	5MF93	GA	May-Jun	bongo,Meth	119	25	22
	6MF93	GA	Sep	Tuck	24	0	2
1994	3MF94	GA	Mar-Apr	bongo, Tuck	49	2	0
	4MF94	BS	Apr	bongo,Tuck	144	37	0

¹ Although larvae of *Lepidopsetta* were collected in neuston and Mocness tows (see "Material examined" section), these collections were not used for abundance calculations and are not listed here.

² Total occurrences for these cruises represent the minimum number collected. Complete records for these cruises are unavailable at this time.